FLORAL ANATOMY OF CHRYSOTHAMNUS (ASTEREAE, COMPOSITAE)[1]

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INTRODUCTION

Details of floral anatomy are presented as part of a series of anatomic studies on *Chrysothamnus*. Although morphological variation in these shrubs of western North America is great enough to warrant the taxonomic designation "difficult genus," relatively little has been written on the anatomy of *Chrysothamnus*, particularly its floral anatomy.

Snow (1945) reported details of floral anatomy for one population of *C. nauseosus*. Recently, some features of floral anatomy of *C. vaseyi* (Anderson, 1963) and *C. bolanderi* (Anderson and Reveal, 1966) were considered in relation to other problems. A paper on embryology (Anderson) is in press.

Species studied are arranged phylogenetically and by sections:

Nauseosi: *C. parryi* (Gray) Greene, *C. nauseosus* (Pallas) Britt.;
Chrysothamnus (*Typici*): *C. linifolius* Greene, *C. spathulatus* L. C. Anders., *C. albidus* (Jones) Greene, *C. greenei* (Gray) Greene, *C. viscidiflorus* (Hook.) Nutt., *C. humilis* Greene;
Pulchelli: *C. vaseyi* (Gray) Greene, *C. molestus* (Blake) L. C. Anders., *C. depressus* Nutt., *C. pulchellus* (Gray) Greene;
Punctati: *C. teretifolius* (Dur. & Hilg.) Hall, *C. paniculatus* (Gray) Hall.

This presentation differs from that of Hall and Clements (1923). *Chrysothamnus gramineus* has been transferred to *Petradoria* (Anderson, 1963) and *C. pyramidatus*, to *Haplopappus* (Blake, 1926). *Chrysothamnus vaseyi* is placed in a different section. New species include *C. molestus* and *C. spathulatus*; *C. linifolius* and *C. humilis* again are recognized as distinct species. Two new combinations are made: C. PARRYI (GRAY) GREENE SSP. **affinis** (A. NELS.) L. C. ANDERS., COMB. NOV. [based on *C. affinis* Nels., Bot. Gaz. 28:374, 1899] and C. NAUSEOSUS (PALLAS) BRITT. SSP. **psilocarpus** (BLAKE) L. C. ANDERS., COMB. NOV. [based on *C. nauseosus* var. *psilocarpus* Blake, J. Wash. Acad. Sci. 27: 376, 1937]. Undescribed taxa are entered in tables parenthetically under the taxon they most closely resemble. Species of two sections of *Haplopappus* (*Macronema* and *Ericameria*) are included for comparison. Relevance of the two sections has been discussed previously (Anderson, 1966; Anderson and Reveal, 1966).

METHODS AND MATERIALS

Fresh materials were generally fixed in formalin-proprionic-alcohol; those used in developmental studies, in Craf V (Sass, 1958). Dried heads were

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treated in 2.5% NaOH to revive cell shape and size, then processed as the fixed materials. Infiltration, embedding, and sectioning in paraplast followed dehydration through a graded tertiary butyl alcohol series.

Heads with considerable sclerenchyma were softened in hydrofluoric acid before being dehydrated. That was particularly useful with more mature heads; otherwise, dehydration and infiltration frequently caused the achenes to dehisce.

Sections were normally made at 12_μ but were cut thinner for developmental series. Staining with safranin was first mordanted with tannic acid followed by ferric chloride (Sass, 1958). Counterstains were either fast green FCF or fast green followed by orange G. Whole flowers were cleared in 2.5% NaOH, dehydrated in a graded ethyl alcohol series, stained in safranin, then transferred to xylene and mounted in permount.

Flowering heads of over 170 populations were used in general studies. Heads from some 50 additional populations were used to confirm distribution of specific features. At least two populations were studied intensively for each taxon. Voucher specimens are in the Kansas State University herbarium unless otherwise indicated; personal collections are indicated by *A*. Utah State University and Rancho Santa Ana Botanic Garden provided garden space, which was deeply appreciated. Mr. Kent Fish prepared many of the slides.

DEVELOPMENTAL ANATOMY

Snow's study (1945) on a population referrable to *C. nauseosus* ssp. *albicaulis* included details of ontogenetic development of floral parts. Her observations are largely applicable to the entire genus; therefore, only features that are new or different are discussd in detail here.

In most species of *Chrysothamnus*, floral organs are initiated in the following sequence: corolla, stamens, pappus, and pistil as figured by Snow (1945). In *C. pulchellus*, the floral primordia differentiate through the sequence of corolla, pappus, stamens, and pistil (Figs. 1-4). The developing primordial lobes of the pappus attain considerable size before the stamens are initiated (Fig. 2).

Precocious development of the pappus is reflected in the mature flower, where the corolla at anthesis is overtopped and often hidden by the copious pappus bristles. That condition may result partially from a slower growth rate in the corolla of that species than in other taxa in the genus. In *C. pulchellus*, the involucre is half its mature length when flower primordia develop, as in Fig. 1. The involucre is nearly full size at time of meiosis. That differential growth rate is less noticeable in *C. depressus*, whereas in other species the developmental rates of involucre and flowers more closely parallel. In fact, in several subspecies of *C. viscidiflorus* the involucral bracts barely surpass flower length at meiosis.

Other species with the *C. pulchellus* pattern of floral ontogeny are *C. depressus*, *C. molestus*, and *C. vaseyi* (all of section *Pulchelli*). In them, pappus development commences just before the stamens, and the pappus does not overtop the corolla in mature flowers.

VASCULAR ANATOMY

Involucre

In most taxa of *C. parryi*, three vascular traces enter each bract (Fig. 5); however, *C. p.* ssp. *parryi*, *C. p.* ssp. *nevadensis*, and *C. p.* ssp. *asper* frequently have five bundles in the larger (outer) bracts. Lateral traces usually extend half of the length of the phyllaries in *C. parryi*; in all other species of the genus the lateral traces terminate at the base of each phyllary. All bracts of *C. nauseosus* ssp. *albicaulis* and *C. n.* ssp. *graveolens* have three traces; other subspecies have three in the outer bracts and one trace in each of the two or three innermost bracts of the head (3/1 pattern).

In section *Chrysothamnus*, *C. linifolius*, *C. albidus*, and *C. greenei* have primarily the three trace per bract pattern, whereas *C. spathulatus* has the 3/1 pattern. Heads of *C. viscidiflorus* vary considerably with *C. v.* ssp. *viscidiflorus*, *C. v.* ssp. *lanceolatus*, and *C. v.* ssp. *planifolius* principally having the 3 pattern and other subspecies having the 3/1 pattern. However, some populations of *C. v.* ssp. *stenophyllus* have only one trace per bract.

In section *Pulchelli*, *C. vaseyi* ranges from the 3 to the 3/1 pattern; *C. molestus* has only the 3/1 pattern, whereas *C. depressus* has the 3/1 or 1 pattern. Possible trends for both expansion and reduction of vascular supply are present in *C. pulchellus* where several populations have the 3 pattern (Fig. 6), but a few have five traces in the outer bracts. Others have 3/1 and one population has the 1 pattern.

Both *C. paniculatus* (Fig. 7) and *C. teretifolius* of section *Punctati* have the 3/1 pattern.

Haplopappus macronema, *H. bloomeri*, and *H. ophitidus* of section *Macronema* have three traces per bract; the lateral traces extend up into the bracts. In *Ericameria*, bracts of *H. propinquus* have the 3 pattern, whereas *H. sonoriensis* and *H. trianthus* have the 3/1 pattern, and *H. pyramidatus* has one trace per bract.

Flower

Venation in flowers of *Chrysothamnus* is relatively advanced for the Compositae. The flower vasculature is derived from the stem as a single bundle. That bundle divides in the base of the achene to first supply the dorsal ovarian bundles, then the laterals, and finally the ventral ovarian bundles. Ovarian bundles range from ten to as few as five. The single ovular trace is a continuation of the vascular supply from the receptacle. In each instance the ovule's vascular supply differed somewhat from Snow's figures (1945). The disc flowers generally have five veins in the corolla, two in the style, and one in each stamen.

The transition from ovarian traces to those of the corolla, stamens, and style can be categorized in five major patterns (Fig. 8, a-e). Observed frequencies of these basic patterns are listed in Table 1. Vascular pattern A has 10 traces in the achene. At the top of the achene the ventral bundle (nearest the axis of the capitulum) and one dorsally positioned each divide to supply a vascular bundle to the style. Those same bundles accompanied by three other ovarian bundles produce the staminal traces before continuing on into the corolla base. The five additional ovarian bundles end blindly at the top of the achene. In most taxa the stylar trace from the ventral ovarian bundle (no. 1 in Fig. 8, a-e) diverges before the one from the dorsal ovarian bundle; however in *C. linifolius* the ventral (adaxial) stylar trace diverges much later. Pattern B also has 10 traces in the achene but differs in that a dorsal ovarian vein terminates as a stylar bundle and does not enter the corolla.

Patterns C and D have a reduction in ovarian trace number with nine to six bundles present in the achene (arbitrarily illustrated as seven in Fig. 8, c-d). In pattern C the dorsal style bundle is associated with a corolla bundle; in D it is not. There is no set pattern regarding which bundles will enter the corolla and which will end blindly at the top of the achene. In flowers with only one extra bundle in the achene, it is usually one on either side of the ventral bundle that ends blindly.

Pattern E, the reduced type, is the one described by Snow (1945). There are only five ovarian bundles so none ends blindly at the top of the achene (see Fig. 24). Bundle no. 3 or 4 may supply the dorsal stylar bundle. The 1-3 pattern of stylar vasculature is more frequent, but both patterns may exist in the same head. In addition, two basic patterns, such as C and E or C and D, can be in different flowers of the same head.

Hall and Clements (1923) state: "Two very unlike types of achenes are encountered in the genus." One is "obscurely 5-angled or terete and 5-nerved . . . the other form which occurs only in *C. vaseyi* and *C. gramineus* . . . is distinctly 10-striate." Actually, there are 5-10 vascular bundles in *C. vaseyi* achenes (Table 1) and only 5 in *C. gramineus* (= *Petradoria discoidea*; Anderson, 1963). Several of the other *Chrysothamnus* species have more than 5 bundles.

Vascular patterns in some *Haplopappus* species are also listed in Table 1. A greatly reduced pattern characterizes *H. pyramidatus*. Only two ovarian bundles are present. The ventral bundle supplies three traces to the corolla and its associated stamens and one to the style, and the dorsal bundle supplies the other two to the corolla and stamens and one to the style.

Several interesting features are found in the "transition region" at the top of the achene where the ovarian bundles supply the vasculature to the corolla, androecium, and style. In nearly all populations the individual ovarian bundles remain distinct and either end blindly or pass into the corolla or style. However, in a few populations representing all species, the ovarian traces fuse at the top of the achene to form a ring of vascular tissue. The coalescence of vascular traces, when present, usually occurs before departure of style bundles; but in *C. pulchellus* the ring is formed after the stylar and staminal traces have departed. Vascular ringing is never so developed that it precludes identification of the basic pattern. In some cases the vascular ring is formed only by the phloem with the xylem strands remaining distinct.

Another departure from the standard vascular patterns is the presence of two additional stylar traces (Fig. 9). They are supplied by lateral ovarian bundles at right angles to the usual dorsal-ventral style traces. The greatest development consists of four traces present up to the style branches with just a single trace entering each branch. Two samples of *C. parryi* ssp. *parryi* and one each of *C. p.* ssp. affin. *attenuatus* (*A 1782*) and *C. linifolius* have this extensive stylar vasculature. Additional style traces, when present, usually terminate at the base of the style or even at the top of the ovary. That condition was found in four subspecies of *C. parryi* and in one sample of each of the following: *C. nauseosus* ssp. *albicaulis*, *C. depressus*, *H. macronema*, and *H. bloomeri*. Additional style traces ending in the ovary and represented only by phloem were found in one sample of each of the following: *C. parryi* ssp. *asper*, *C. p.* ssp. *attenuatus*, *C. nauseosus* ssp. *bernardinus*, *C. viscidiflorus* ssp. *lanceolatus*, and *C. v.* ssp. *viscidiflorus*.

Pappus in *Chrysothamnus* does not contain vasculature. Traces diverged toward the base of pappus bristles were observed only in one population of *C. parryi* ssp. *vulcanicus* (Fig. 32).

Ray flowers, long considered foreign to *Chrysothamnus*, are present only in two populations of *C. spathulatus* (Fig. 11). They are found in nearly every head on plants from canyons of Guadalupe Mountain, Culberson County, Texas (the southern-most point of the species). Plants from the Jicarilla Mountains in Lincoln County, New Mexico, represent the northern-most population of the species; those only occasionally have ray flowers. In both cases rays are no larger than the disc flowers and have a long tube and narrow, often involute limb. The commonest vasculature for these inconspicuous flowers is six ovarian bundles and four in the corolla with two in the style (diagrammatically represented in Fig. 8, f). In one case the adaxial vein of the corolla tube divided at the sinus to form the two laterals of the five-veined limb. Four veins were found in the tube (Fig. 11) and limb of all other samples. The androecium was lacking in all ray flowers.

HISTOLOGY

Involucre

Phyllaries are not treated in great detail because they are similar to the leaves and share many features with the vegetative anatomy of the plants (subject of a future paper). The most notable difference anatomically is the extensive development of sclerenchyma in the phyllaries.

The involucral bracts were studied at three levels: 1.) At a short distance below the tip of the bract, the tissue composition near the midrib usually has one or two rows of parenchyma adjacent to the adaxial epidermis, followed by two or three rows of sclerenchyma, and two or three rows of palisade parenchyma next to the abaxial epidermis. This palisade is responsible for the "sub-apical green spot" of the bract (outermost bract in Fig. 6). Inner bracts of the involucre lack this chlorenchyma. Some samples lack rows of sclerenchyma but have islands of a few fibers scattered abaxially in the bract tip. 2.) Midway down the length of the bract, tissues contain from three to six rows of sclerenchyma next to the outer epidermis. 3.) The bract varies most near its base. In *C. parryi* the "mesophyll" is 10-18 cells thick and entirely parenchymatous (Fig. 5). At the other extreme the bract is thinner and less leaf-like, having three rows of adaxial parenchyma and eight rows of abaxial sclerenchyma; this pattern is found in *C. paniculatus*.

Percentage of sclerenchyma to total mesophyll (averaged from the three levels) is from 40-60% for most taxa. The least sclerenchyma is found in *C. parryi* ssp. *parryi* (16%); most subspecies of *C. parryi* have 25-45% sclerenchyma. Greatest development of sclerenchyma is in section *Punctati*. *Chrysothamnus paniculatus* has 68% and *C. teretifolius*, 74%; in the latter the large-celled adaxial parenchyma have thick walls from secondary sclerosis.

Large secretory canals are usually found abaxially in the midrib of each bract (Figs. 5-7). The lateral bract bundles also have secretory canals associated with them in the following: *C. parryi* ssp. *parryi*, *C. p.* ssp. *asper*, *C. p.* ssp. *nevadensis*, *C. p.* ssp. *vulcanicus*, and occasionally in *C. linifolius*. A reduction of secretory apparatus is found in *C. paniculatus*, *C. teretifolius*, and a few subspecies of *C. nauseosus* and *C. viscidiflorus*. In the first, the tips of the outer bracts lack secretory canals; in the remaining taxa mentioned the canals are absent from the basal portions of the inner bracts.

Trichomes are abundant on developing bracts (Figs. 1-2), and nearly all taxa have some at maturity. Glandular trichomes are present on most taxa; they are usually on the adaxial surface of the bract, but in section *Punctati* they are abaxially located (Fig. 7). Section *Pulchelli* is characterized by having short, stiff nonglandular trichomes on the abaxial phyllary epidermis. Those hairs are frequent on *C. depressus*, less so on *C. molestus*, and much rarer on the remaining species of the section. All but *C. depressus* have adaxially located glandular hairs as well.

Members of section *Nauseosi* have long, uniseriate, nonglandular trichomes on their stems. Phyllaries may have either glandular or nonglandular hairs or both. Most taxa of *C. parryi* have adaxial glandular hairs and abaxial nonglandular hairs; *C. p.* ssp. *latior*, however, lacks the latter. In *C. nauseosus* the "gray forms" (*C. n.* ssp. *albicaulis*, *C. n.* ssp. *hololeucus*, etc.) have nonglandular trichomes exclusively, whereas the "green forms" (*C. n.* ssp. *consimilis*, *C. n.* ssp. *graveolens*, etc.) have only glandular trichomes.

Flower

Trichomes. The taxa vary as to kind, size, and quantity of trichomes they bear; vesture is tabulated in Table 1 and illustrated in Figs. 13-23. Explanation of symbols in Table 1 is: g, glandular; n, nonglandular; + +, abundant; +, frequent; —, rare.

Trichomes may be found on the achene, on the corolla tube, and on the tips of corolla lobes. The commonest trichome on the achene is the "twin-hair" (Zwillingshaare). The hairs are four-celled, biseriate, and nonglandular (Figs. 13-14); they have thick walls that are anisotropic under polarized light. The twin-hairs range from less than 100 to over 700 long and are abundant when they are the only type found on the achene. They are much less frequent and somewhat caducous in *C. spathulatus*.

Truly glabrous achenes, i.e., ontogenetically so, are found only in certain taxa of *C. nauseosus* (see Table 1). One taxon not listed in the table, *C. n.* var. *petrophilus*, also has glabrous achenes—the only feature that separates it from *C. n.* ssp. *consimilis*. Achenes of section *Pulchelli* are often referred to as glabrous. However, excluding *C. pulchellus*, all species have glandular trichomes scattered over the distal half of the achene (Figs. 15-16); in addition, a few short twin-hairs usually are present. In *C. pulchellus*, the developing ovaries often have nonglandular trichomes. Mature achenes may be glabrous (Fig. 6), or a few twin-hairs may persist. *Haplopappus bloomeri* and *H. ophitidus* also have nearly glabrous achenes.

An intermediate pattern is found in *C. albidus* and *C. humilis*. Both have abundant twin-hair groups on the achenes, which mask the glandular trichomes also present (Fig. 31).

Trichome occurrence on the corolla largely follows sectional lines in *Chrysothamnus*. Hairs on the corolla tube are relatively abundant in section *Nauseosi*. The hairs are elongate biseriates, often termed villi (Figs. 17-19); both nonglandular and glandular forms may be present. In *C. parryi* the distinction between the two categories is nearly lacking due to the narrow heads on the glandular trichomes (Fig. 18). Occasionally, a few anisotropic uniseriate hairs are present on the corolla tube as in *C. nauseosus* ssp. affin. *turbinatus* (*A 1771*).

Hairs on the corolla tube are infrequent in sections *Chrysothamnus* and *Pulchelli*, being found only in *C. humilis* (Fig. 21) and some subspecies of *C. viscidiflorus* and in *C. molestus*, respectively. In section *Punctati* glandular hairs are common on the corolla tube (Fig. 22); they are shorter and more clavate than the glandular hairs in the *Nauseosi*.

The corolla lobes in section *Nauseosi* often bear trichomes (Table 1). Hall and Clements (1923) listed this feature for only three taxa. The usual form is a long uniseriate hair that is anisotropic (Fig. 23). Length determinations are hampered by hairs breaking when handled; many are over a millimeter long. Corolla lobes are glabrous in *C. nauseosus* ssp. *albicaulis* over most of its range; however, two widely separated populations of this taxon have villous corolla lobes. They are from Kane County, Utah (*A 1725*), and Walla Walla County, Washington (*E. F. Anderson 2071*). Biseriate hairs on corolla lobes, when present, are usually glandular and isotropic, but on *C. n.* ssp. affin. *turbinatus* (*A 1778*) biseriate nonglandular hairs occur as well as uniseriate ones. The biseriates are similar to the twin-hairs of the achene except they are shorter and isotropic. Glandular trichomes are particularly abundant on corolla lobes of *H. pyramidatus* (Table 1).

All species have epidermal pappilae, especially at the tips of corolla lobes. In some, such as *C. parryi* ssp. *parryi* and *C. nauseosus* ssp. *bernardinus*, the pappilae extend 90_μ from the epidermis. Many species have lignified epidermal cells at corolla tips that are anisotropic.

Secretory apparatus. The flowers may contain secretory canals associated with vascular tissue in four areas: the ovary wall of the achene, the corolla tube from the point of staminal departure to the tips of their lobes, the upper part of the style and its branches, and in the anthers. Secretory canals in the anthers are found only in some populations of *C. parryi* ssp. *parryi* (Fig. 12). Abundance of secretory canals in the three other regions of the flower is listed in Table 1. Determination of frequency (++, abundant; +, frequent; —, rare; 0, absent) was made at seven zones (Fig. 24); zones I and II are from the achene, III-V from the corolla, and VI and VII from the style.

Members of *Nauseosi* have the greatest development of secretory canals, whereas canals are entirely absent in flowers of *C. albidus* and *C. paniculatus*. Distribution of canals follows section lines fairly well. *Chrysothamnus* and *Pulchelli* have no canals in the style (zones VI and VII, Fig. 24). Nonetheless, *Punctati*, a rather well-defined section from external morphology, has discordant species as far as secretory apparatus is concerned.

Tissue composition. Most taxa from all sections have well developed sclereids representing the seed coat (ovule wall) in the ovary. The sclereids have thickened radial and especially outer tangential walls (Figs. 25-28). In sections *Chrysothamnus* and *Pulchelli* there is a tendency for greater sclerification of the ovary wall as seen in clusters of thick-walled cells in achenes of *C. spathulatus* (Fig. 27). The entire ovary wall is sclerosed at maturity in *C. pulchellus* (Fig. 28); achenes of that species also have the thickest ovary walls in the genus.

Ground tissue of the corolla is parenchymatous. In the corolla lobes the parenchyma is frequently disrupted near the veins by lacunae. Tissue thickness was measured at three points (Fig. 24, levels A-C) and recorded in Table 1. Level A is at the corolla base just at the top of the nectaries, level B is just above the point of staminal filament departure, and C is just below the sinuses of the corolla lobes. Section *Pulchelli* has the thickest corollas, followed by *Chrysothamnus*.

Staminal filaments often have protoxylem lacunae. Staminal endothecium is as follows. In the anthers the outer tangential and radial walls of the hypodermis have the characteristic fibrous thickenings. On the abaxial side of the connective below the anther and in the sterile appendage above the anther, all walls of the hypodermis and the inner walls of the epidermis are differentiated as endothecium. Both surfaces of the anther appendage have endothecium in *C. humilis*.

Endothecial thickenings in the anther wall follow the patterns described by Dormer (1962). All three categories, i.e., polarized, radial, and transitional tissue, are represented. The polarized tissue has two to three prominent vertical bars on the faces of each cell wall. Although polarized fibrous thickenings are predominant in the family as a whole, radial tissue with horizontal bars is the most abundant in *Chrysothamnus*, and that is the basic type in the Astereae (Dormer, 1962).

Cells of the corolla base, and particularly the style base, develop heavy secondary walls as the flowers pass anthesis (Fig. 10). That tendency is most pronounced in *Pulchelli* and *Chrysothamnus*.

A continuous ring of tissue around the base of the style rises into five prominent nectaries (Fig. 29). They are alternate to the stamen positions and vary considerably in size and shape. Size is perhaps best measured in relation to flower size; that was done by measuring style length up to the base of the style branches. Longest nectaries, by that relationship, are in *C. albidus*; they are 4.2% of the unbranched style length. Other taxa with large nectaries (3.8%) are *C. paniculatus* (Fig. 30) and *C. nauseosus* ssp. *consimilis*. Most nectaries range from 1.5 to 2.5% of the unbranched style length. Very small nectaries in the form of low humps (less than 1.0% the style length) are found in *C. depressus*, *C. molestus*, *C. humilis* (Fig. 31) and some subspecies of *C. viscidiflorus*. Most nectaries are partially fused with the style base as in *C. parryi* (Fig. 32).

ENVIRONMENTAL EFFECTS ON ANATOMY

Features studied in original collections were compared with those produced in plants in experimental gardens at Logan, Utah, and Claremont, California. Relative genetic uniformity was obtained by transplants or through progeny. Seedlings were considered genetically close to original collections as the taxa are basically inbreeding (Anderson, 1966).

Table 2 includes topographic, climatological, and edaphic data for the gardens; Table 3, features of the original localities. Climatological data for the gardens were obtained at the garden sites and reflect climates for one year prior to harvest; plants in the Claremont garden were irrigated only as needed to insure establishment (Claremont precipitation averages 19-20" annually). Climatological data for original collection sites are based on 20-year averages; when recording stations were farther than 10 miles from the collection site, data are considered estimates (prefix E in Table 3) for the collection sites.

Environmental extremes between the two gardens were probably sufficient to produce the main amplitude of anatomic variation possible for each collection's genotype. Differences in temperature are particularly noteworthy: mean monthly minimums at Claremont were never below 40° F.; whereas mean monthly maximums at Logan were near or below freezing for three months.

Floral features are included in Table 4 (same format at Table 1) only for collections represented in both gardens; however, additional taxa were used in garden studies. Most propagations survived and flowered, but plants of *C. paniculatus* died in the Logan garden during the first growing season. Vigor in surviving plants was usually reduced when the gardens differed considerably from the natural habitat. External morphology varied much more than did internal anatomy. The most sensitive floral feature is flower number in *C. parryi*. In the Claremont garden, different plants of *C. parryi* ssp. *parryi* averaged from five to nine flowers per head.

Only minor fluctuations occurred in floral anatomy in the gardens, but trichomes of *C. vaseyi* achenes were an exception. The achenes of *C. depressus*, *C. molestus*, and *C. vaseyi* are frequently described as glabrous; however, they all have glandular and nonglandular trichomes at the distal end of the achene (Table 1). The glandular hairs are readily apparent under a hand lens; the less frequent nonglandular hairs were first observed in sectioned materials under the microscope. The nonglandular trichomes (twin-hairs) became more abundant in the garden propagations of *C. vaseyi*. In the Logan garden, they equalled the glandular hairs in frequency and completely covered the achenes in the Claremont garden.

ANATOMY OF HYBRIDS

Hybridization in *Chrysothamnus* is infrequent. In the absence of gross chromosomal irregularities in meiosis in presumed hybrids (Anderson, 1966), anatomic comparisons are valuable in determining hybridity. Such comparisons have been made for *C. bolanderi* (Anderson and Reveal, 1966).

Putative hybrids between *C. parryi* ssp. *parryi* and *C. nauseosus* ssp. *nauseosus* were recorded earlier (Anderson, 1966); features of their floral anatomy are listed in Table 5 (format that of Table 1). In addition, glandular trichomes on the corolla lobes were most abundant in *C. parryi* ssp. *parryi*, intermediate in frequency in the hybrids, and least abundant in *C. nauseosus* ssp. *nauseosus*. The hybrids were also intermediate in nectary size; *C. nauseosus* had the largest, and *C. parryi* the smallest.

Involucral bract structure and alignment suggest the type collection of *C. nauseosus* ssp. *viscosus* (*Munz 12689*, RSA) is an intergeneric cross between some population of *C. nauseosus* and a species of *Haplopappus*. Flower number (Table 1) reinforces the probability of hybridity.

An intersectional hybrid was obtained in the Claremont garden. Seed from *C. albidus* produced a plant with pannose tomentum characteristic of stems of *C. nauseosus*; flower color (pale lemon yellow) was intermediate between the putative parents. Several floral features in that propagation, but absent in *C. albidus*, point to hybridity: secretory canals in the achenes, absence of glandular trichomes on the achenes, and trichomes on the corolla tube.

TERATOLOGICAL ANATOMY

Normal and abnormal flowers are not mutually exclusive categories. Determining teratisms is largely subjective. Further, use of teratism in phylogenetic studies is widely debated (Takhtajan, 1954). Nevertheless, the intensive nature of this study enables a better determination of the extent and significance of anatomic teratologies.

Frequency of certain teratological types are listed in Table 6; more than one type can occur in the same head. Additional types are discussed in the text, and some are illustrated in Figs. 33-37. Six-merous flowers and flowers with additional corolla vasculature (midveins) are the most frequent forms. Unfused lateral veins in the corolla (Fig. 35) are restricted to *Nauseosi*. Teratisms vary in degree of occurrence. In *A 2714* (Fig. 34), every flower of the four heads sectioned has midveins, whereas only one abnormal flower was found in *A 1606* (Figs. 36-37) in the two heads sectioned.

Heads with one or more flowers positioned among the involucral bracts in addition to the normally-positioned central group occur in some populations of *C. linifolius* (*A 920, A 1860*). An extreme case (Fig. 33) has four such flowers. They are abnormal in anatomy as well as position. Some have free floral parts that are normally fused in composites; others have abnormal fusions, such as stamens with the style. The flowers produced in the usual position inside the bracts are normal.

Flowers of *A 2714* (*C. viscidiflorus* ssp. *viscidiflorus*), in addition to 10 veins in the corolla tube, have unusual growths inside the corolla tube opposite the extra veins (Fig. 34). They are possibly staminodes. Such structures were seen in one or two flowers of other taxa; in *A 2714*, they appear in all flowers. Secretory canals are associated with the extra vasculature, but not with the normally-positioned five bundles (Fig. 34). Those secretory canals extend down the corolla tube well below the point of staminal departure, which is much greater distribution than normal (see Fig. 24, zone III).

One flower of *A 1606* (*C. humilis*) has two ovules, and in addition to the outer row of ovarian bundles associated with the corolla vasculature, there is an inner, strictly gynoecial bundle (Fig. 36). That inner bundle enters the trifid style; a total of six bundles enter the style base (Fig. 37).

DISCUSSION

To properly evaluate morphological features for use in biosystematics, one must first determine the relative stability of those features. That may be accomplished by garden studies. Uniform gardens allow comparison of behavior of plants with different heredity in the same environment; growth of the plants in varied environments permits observation of the interplay between heredity and environment. The work of Clausen, Keck, and Hiesey (1940) is a classic in that field; however, to my knowledge, the technique has not been extensively applied to anatomic studies.

Gardens used in this study presented greater environmental extremes than most taxa encounter in nature (Table 2); therefore, anatomic variation found in the gardens likely is greater than that found in natural populations. It follows, then, that features that remain constant, or relatively so, in the three environments (Table 4) can be validly used for taxonomic comparisons.

Stability of internal structures is generally conceded to be greater than that in features of external morphology. The concept is upheld in this study. Tissue composition, vasculature, and particularly the amount and distribution of secretory canals are extremely constant. The greatest variability is found in achenial trichomes of *C. vaseyi.* Here the variation is quantitative rather than qualitative. The increase in twin-hairs was so great in the Claremont garden that it completely masked the glandular achenes. Both gardens were outside the natural range of *C. vaseyi.* Apparently differing environments enhanced different expressions of the genotype.

The close genetic control of features of floral anatomy permits use of the data at all taxonomic levels to help determine distinctiveness of taxa and to determine phylogenetic relationships.

Taxonomy

Subspecies. Data from floral anatomy support current taxonomic interpretations in many cases; however, two notable exceptions are discussed here. Hall and Clements (1923) described three subspecies for *C. pulchellus.* Floral anatomy of that species varies sufficiently to imply subspecies, but the patterns of variability do not coincide with the subspecies of Hall and Clements. Study of the problem is continuing.

Perhaps the greatest value of data from floral anatomy at this level is clarification of the infraspecific relationships in *C. parryi.* Hall and Clements (1923) list 10 subspecies. Their and my concepts of phylogeny are reproduced in Fig. 38, left and right, respectively. Floral anatomy contributed to my concept. Hall and Clements (1923, pp. 203-206) describe two major divisions of *C. parryi*: 1.) the primitive stock that developed into ssp. *parryi* in the Rocky Mountains and ssp. *bolanderi, latior,* and *imulus* in the Sierra Nevada; 2.) the second division composed of two "apparently nautral groups"—the *asper* line and the *howardii* line. Closeness of subspecies in their phylogenetic chart is considered to reflect genetic relationship.

Several major differences between the two schemes (Fig. 38) are apparent. The hybrid, *C. bolanderi,* is not included in my concept as its origin does not involve taxa of *C. parryi* (Anderson and Reveal, 1966). Hall and Clements considered ssp. *affinis* as a minor variation of ssp. *attenuatus; affinis* is more appropriately allied with ssp. *parryi* as absence of corolla lobe trichomes indicates (Table 1). The *asper* line of Hall and Clements is unnatural, and ssp. *vulcanicus* is considered much less specialized than they suggested. The four undescribed taxa of the *C. parryi* complex listed in Table 1 are very specialized populations, more so than any shown in Fig. 38.

Species. Several species have been placed in *C. viscidiflorus; C. molestus* (Blake, 1940) and *C. spathulatus* (as *ludens;* Shinners, 1964) have been considered varieties of *C. viscidiflorus,* and *C. humilis* and *C. linifolius,* as subspecies (Hall and Clements, 1923).

Chrysothamnus molestus is very distinct from *C. viscidiflorus* and belongs to a different section of the genus. The closely related *C. spathulatus* and *C. linifolius* differ from *C. viscidiflorus* in that the first species has nearly glabrous achenes, fewer secretory canals, and, occasionally, ray flowers, and the second has more flowers per head and more vasculature and secretory canals in the inflorescence. Achenes of *C. humilis* have a distinctive trichome complement (Table 1), and heads have fewer flowers. Other distinguishing features of these taxa have been enumerated (Anderson, 1964). On the other hand, floral anatomy does not support the distinctness of *C. axillaris* (Keck, 1958) as a separate species; it varies only slightly from *C. viscidiflorus* ssp. *stenophyllus*.

Section. Of the four sections of *Chrysothamnus*, *Pulchelli* is the most strikingly delineated by floral anatomy, particularly in trichomes and floral ontogeny. *Nauseosi* is characterized by presence of stylar secretory canals and usually has trichomes on the corolla tube. Sections *Chrysothamnus* and *Pulchelli* lack stylar secretory canals and have trichomes on the corolla tubes in only a few taxa. Involucral structure and trichomes are uniform and distinctive in *Punctati*; however, its species are very dissimilar in secretory canal distribution.

Genus. Many students of Compositae agree *Chrysothamnus* is closely related to and possibly derived from *Haplopappus*, but views vary as to the closest point of relationship. Hall and Clements (1923) propose a close affinity between *C. paniculatus* and *H. sonoriensis* of section *Ericameria*. Others (Gray, 1873; Greene, 1895) suggest *C. parryi* is most primitive and close to *H. macronema* of section *Macronema*.

Chrysothamnus paniculatus and *Haplopappus sonoriensis* differ conspicuously in floral anatomy in that *H. sonoriensis* and other taxa of section *Ericameria* have well developed secretory canals in the achenes and corollas (except *H. pyramidatus*, which is anomalous in other ways). Further, *H. sonoriensis* has glandular trichomes on the involucral bracts that are terminated by a long thickwalled, finger-like cell. That kind of trichome is present on the receptacle of *H. laricifolius* (*A 3038*) but absent in all *Chrysothamni*.

Secretory canal distribution and trichome patterns are similar in *C. parryi* and *H. macronema*. That, coupled with details of the biology of *C. bolanderi* (Anderson and Reveal, 1966), suggest the *C. parryi—H. macronema* connecting point between the two genera is the closer.

Phylogeny

Determination of evolutionary trends in the genus can be made by comparing floral anatomy of *Chrysothamnus* to that of other Compositae and by comparing it with data on *Chrysothamnus* from such other areas as morphology and cytology.

Col (1904) found an evolutionary trend in the secretory apparatus of Compositae. Less specialized taxa have more secretory canals than do the more advanced taxa. In *Chrysothamnus*, *C. parryi* ssp. *parryi* and ssp. *vulcanicus* (Table 1) have the most floral secretory canals; *C. albidus* and *C. paniculatus* have the least (present only in the involucre).

Several writers (Babcock, 1947; DeJong, 1965; Koch, 1930; Stebbins, 1940) have noted that more vascular strands in the achenes represent a primitive feature in various Compositae. In *Chrysothamnus*, several subspecies of *C. parryi* and a few of *C. nauseosus* consistently have more ovarian vascular bundles than do other taxa.

The most primitive composite flowers have 15 veins in the corolla, one midvein and two laterals per member of the 5-merous flower (Carlquist, 1961). Phylogenetic trends include loss of the midvein and fusion of adjacent laterals to produce a 5-veined corolla. Floral teratologies (Table 6) are instructive if they reflect phylogeny, either as atavisms or vestiges. Greater vascularization is indicated by unfused laterals and extra corolla veins (midveins); tristyly and 6-merous flowers might relate to extra vascularization in those parts. *Nauseosi*, particularly *C. parryi*, has the greatest amount of these combined teratisms. Since evolutionary trends adduced from floral aberrations are positively correlated with those from other areas, their use seems acceptable for *Chrysothamnus*. Similarly, the 4-merous flower as in *C. viscidiflorus* and *C. humilis* might reflect a continuing trend of reduction and specialization.

A correlation between amounts of vascularization and secretory canals is probable; it is definitely suggested in teratological forms. Corollas of *C. viscidiflorus* normally lack secretory canals, but in *A 2714* they are present along the extra (midvein) bundles (Fig. 34) and extend down the corolla tube past the point of staminal insertion.

Cronquist, in reviewing phylogeny in Compositae (1955), suggested several features as being primitive in the family. The following are appropriate to the discussion here: heads few, each with many flowers; involucres leafy, several seriate; and rays present, pistillate, fertile. In *Chrysothamnus*, the first two features apply best to *C. parryi* ssp. *parryi*. The inflorescence has fewer heads than in most taxa; each head contains 10—20 flowers, and the phyllaries are more herbaceous and leaf-like than in any other taxa. Ray flowers are found occasionally only in *C. spathulatus*; however, that Compositae probably lacked ray flowers primitively (Carlquist, 1961) does not alter the apparent primitive position of *C. parryi* ssp. *parryi*. Data from cytology support that position (Anderson, 1969); *Chrysothamnus parryi* ssp. *parryi* has the least specialized karyotype known to the genus.

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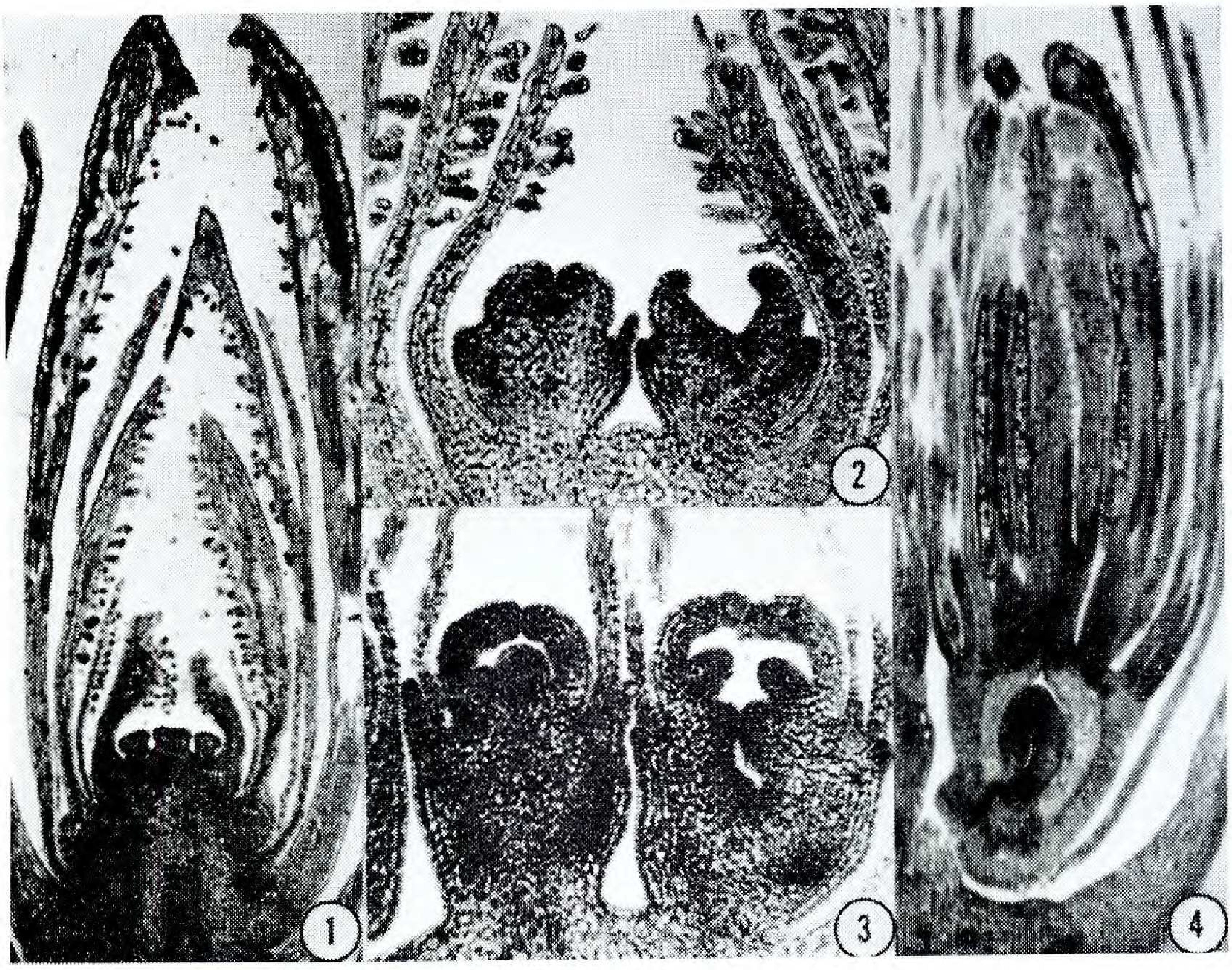
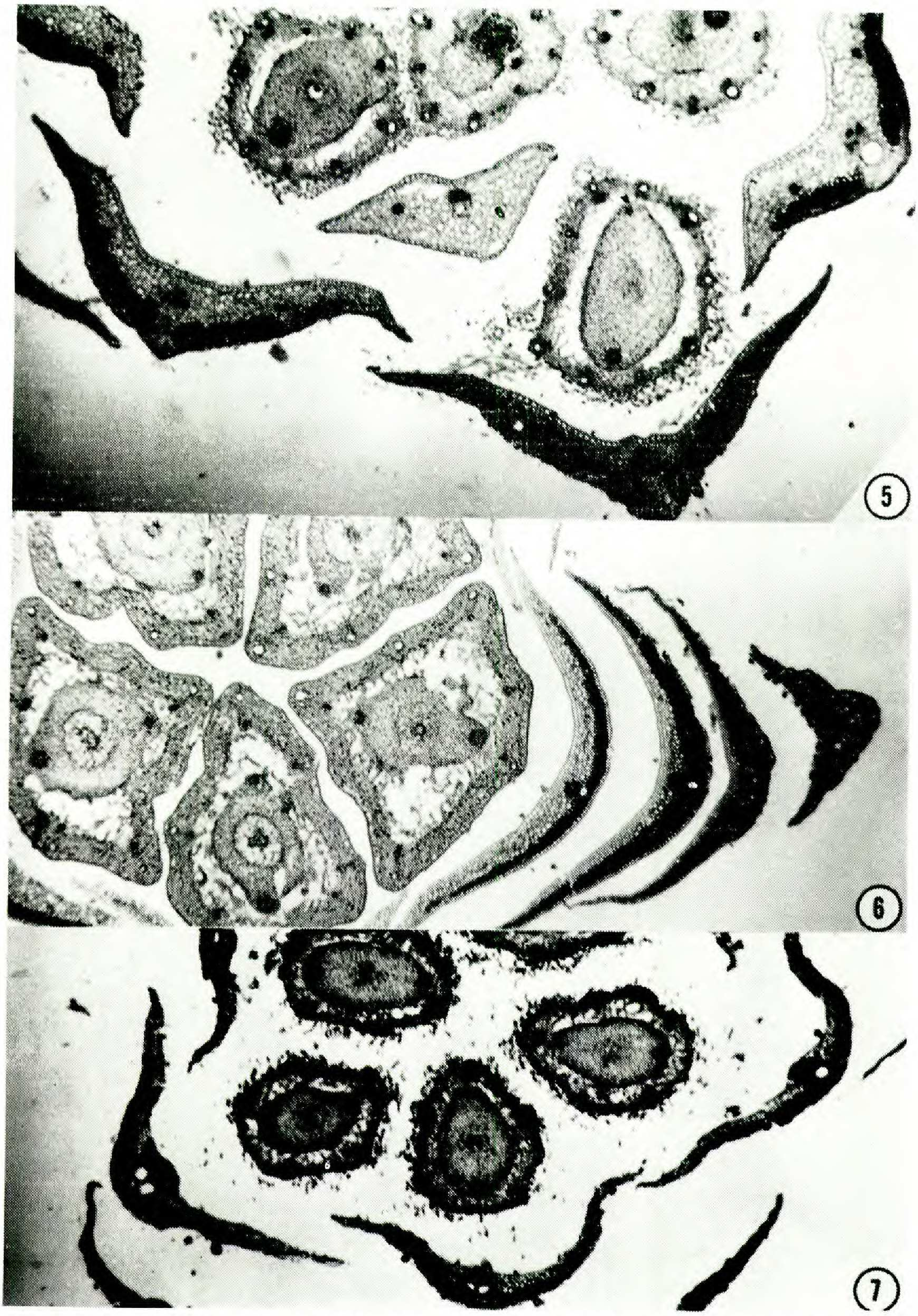


Figs. 1—4. Floral ontogeny in *C. pulchellus* (*A 2590*). Fig. 1. Longisection of head 5 mm long showing three flower primordia and extensive bract development. Fig. 2. Portion of head 6 mm long showing two developing flowers with corolla and pappus differentiated. Fig. 3. Flowers from head 7 mm long showing extensive pappus and initial development of androecium and ovule. Fig. 4. Portion of head 11 mm long with flower undergoing meiosis in megaspore mother cell. Figs. 1, 4, X 30. Figs. 2-3, X 115.



Figs. 5—7. Transections of heads through the achenes. Fig. 5. *C. parryi* ssp. *parryi* (*A 2681*), each achene with 10 vascular bundles and bracts with 3; inner bracts completely devoid of sclerenchyma. Fig. 6. Glabrous achenes of *C. pulchellus* (*A 2995*) with 5-6 bundles; note strong alignment of involucral bracts. Fig. 7. *C. paniculatus* (*A 1931*), achenes with 5-6 bundles. Figs. 5—7, X 37.

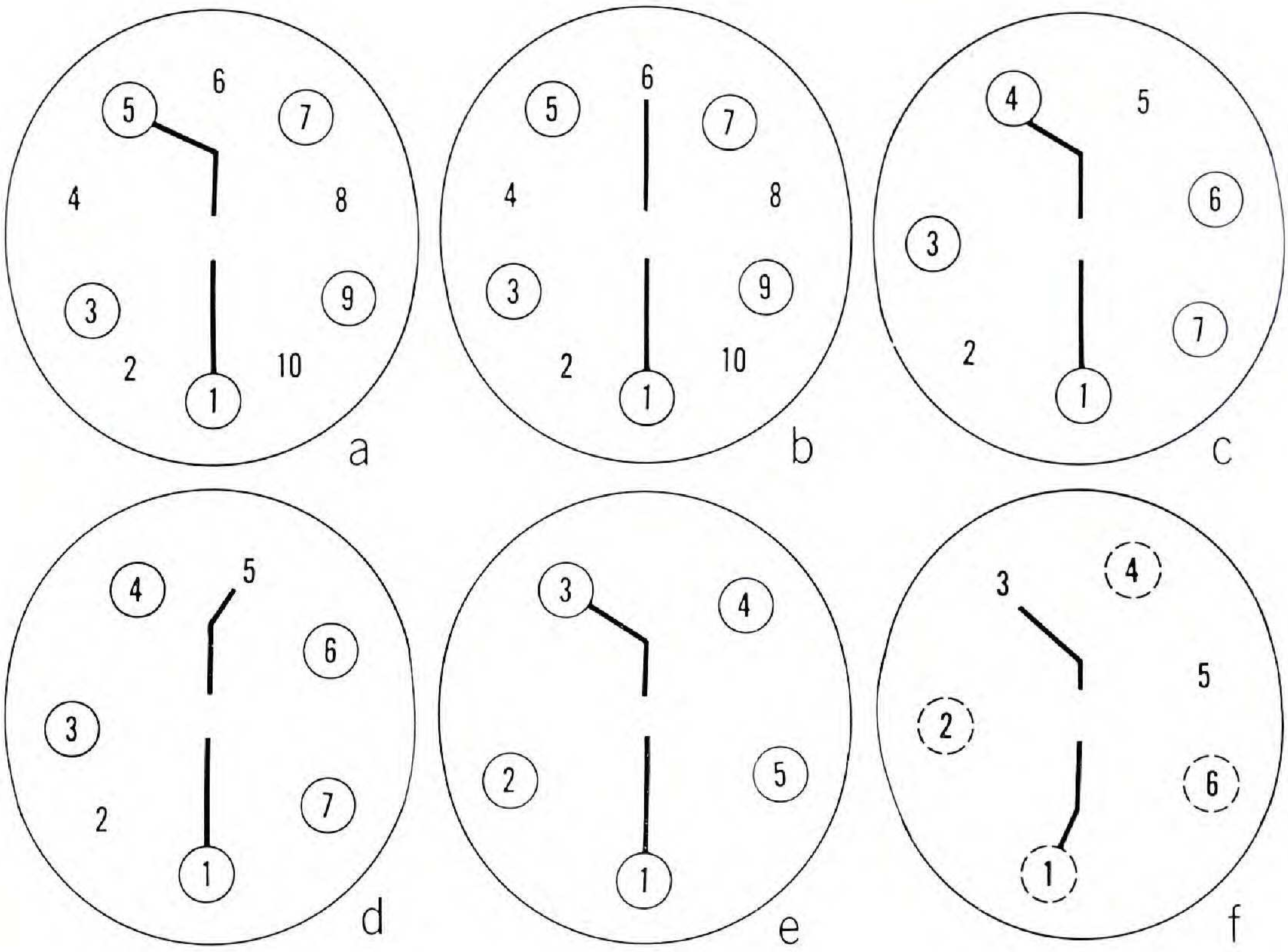
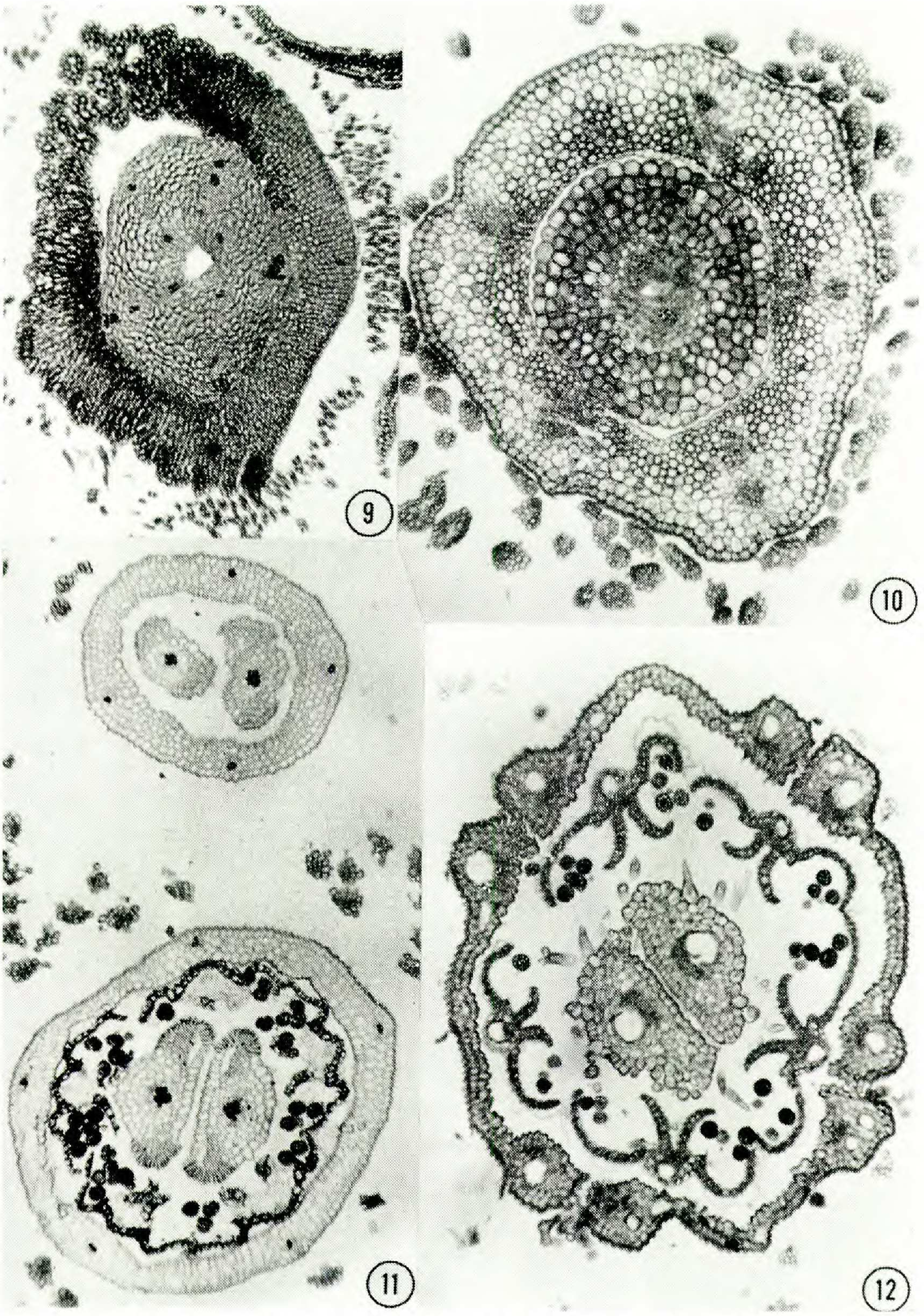
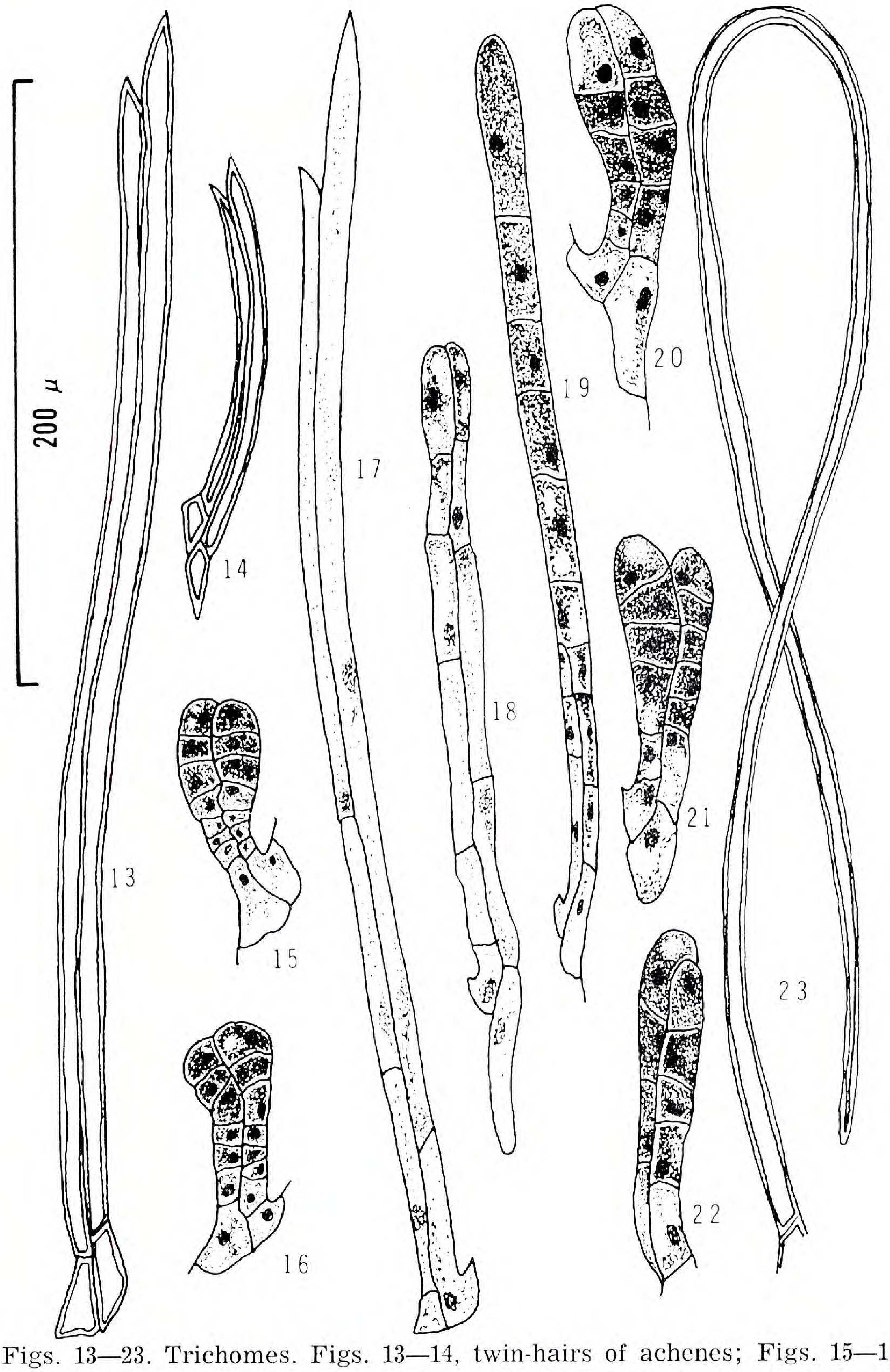


Fig. 8. Diagrammatic patterns of ovarian vasculature and transition to corolla, stamens, and style. Fig. 8a-8e. Disc flowers. Numbers represent ovarian vascular bundles; encircled numbers are those that divide to supply the corolla and androecium, and solid lines indicate the ovarian bundles that supply traces to the style. Fig. 8f. Ray flower; broken circles represent ovarian bundles that continue into corolla (androecium absent).



Figs. 9—12. Flower transections. Fig. 9. Transition region at top of achene of *C. nauseosus* ssp. *albicaulis* (*A 2083*) with ring of pappus, five bundles of the corolla base, and four at the style base. Fig. 10. *C. depressus* (*A 993*), cells of corolla and style base with heavy secondary walls. Fig. 11. Ray and disc flowers of *C. spathulatus* (*A 3209*), both lacking secretory canals. Fig. 12. *C. parryi* ssp. *parryi* (*A 2681*), secretory canals present in corolla lobes, anthers, and style branches. Figs. 9—12, X 86.



Figs. 13—23. Trichomes. Figs. 13—14, twin-hairs of achenes; Figs. 15—16, glandular hairs of achenes; Figs. 17—19, villi of corolla tubes; Figs. 20—22, glandular hairs of corolla tubes; Fig. 23, shag-hair of corolla lobe. Fig. 13. *C. viscidiflorus* ssp. *stenophyllus* (*A 1746*). Figs. 14—15. *C. vaseyi* (*A 936* and *A 1002*, respectively). Fig. 16. *C. molestus* (*A 3148*). Figs. 17—18. *C. parryi* ssp. *asper* (*A 1919* and *A 2043*, respectively). Fig. 19. *C. nauseosus* ssp. *albicaulis* (*A 2001*). Fig. 20. *C. viscidiflorus* ssp. *lanceolatus* (*A 2735*). Fig. 21. *C. humilis* (*A 2950*). Fig. 22. *C. paniculatus* (*A 1925*). Fig. 23. *C. parryi* ssp. *nevadensis* (*A 2952*).

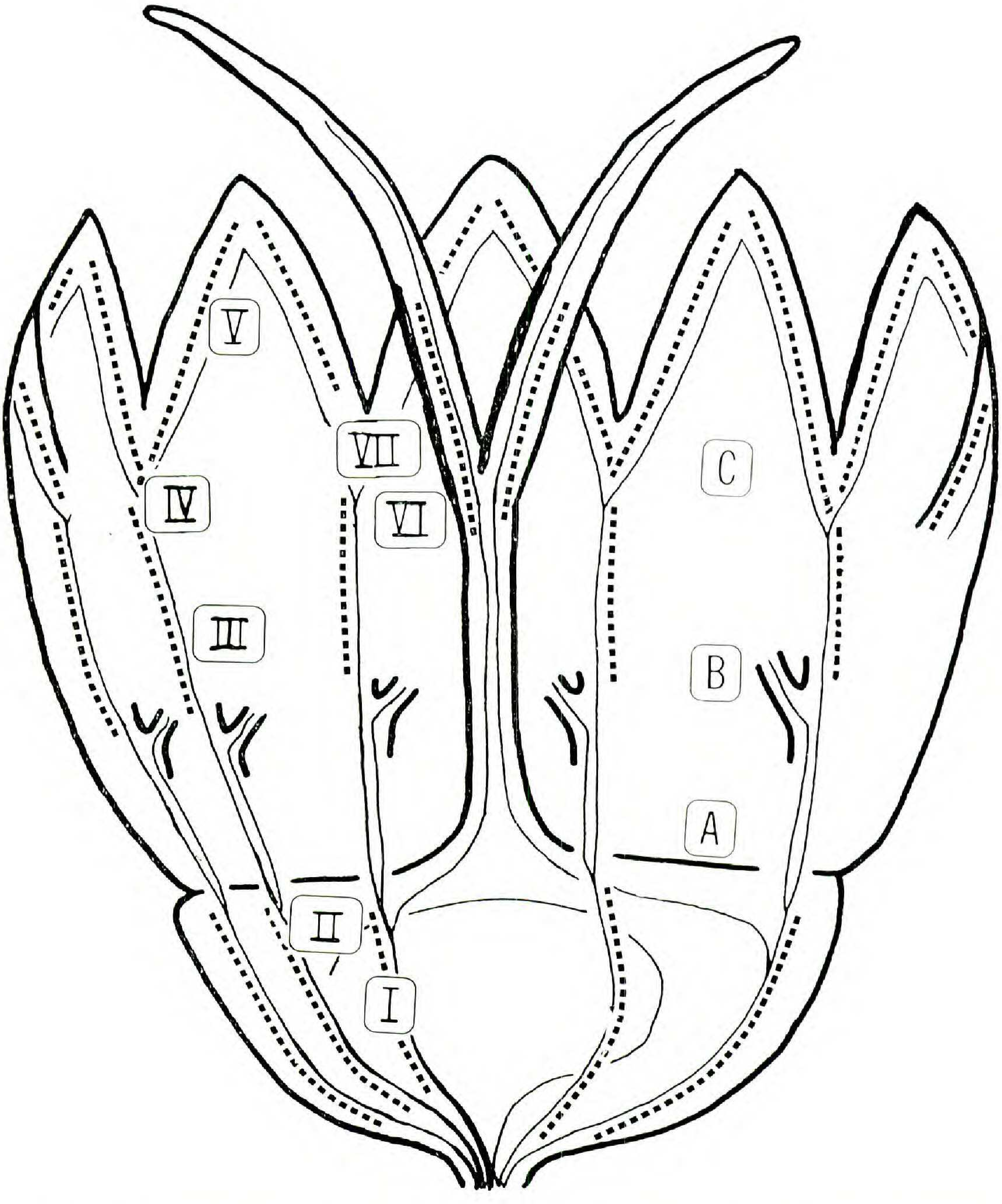
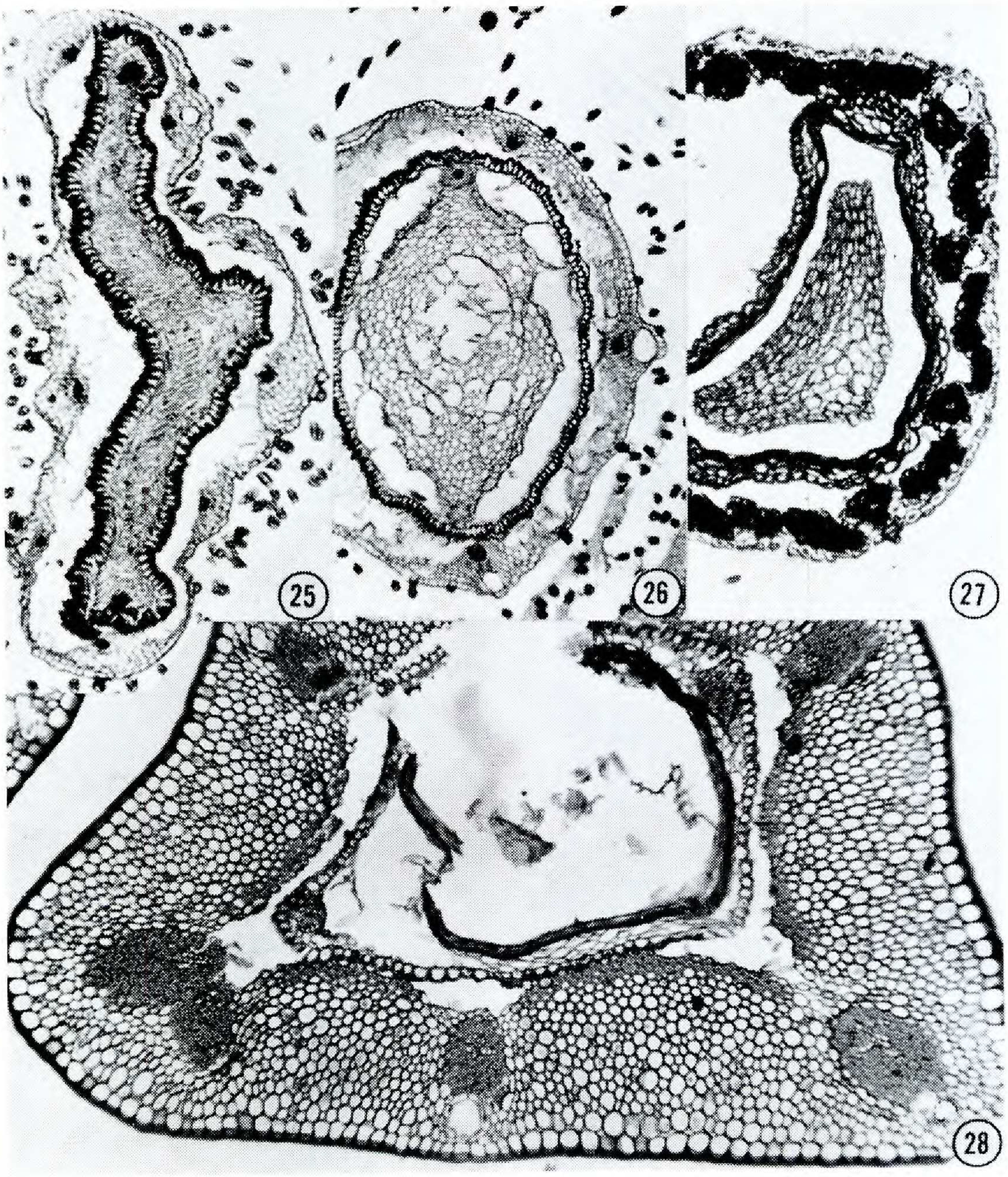
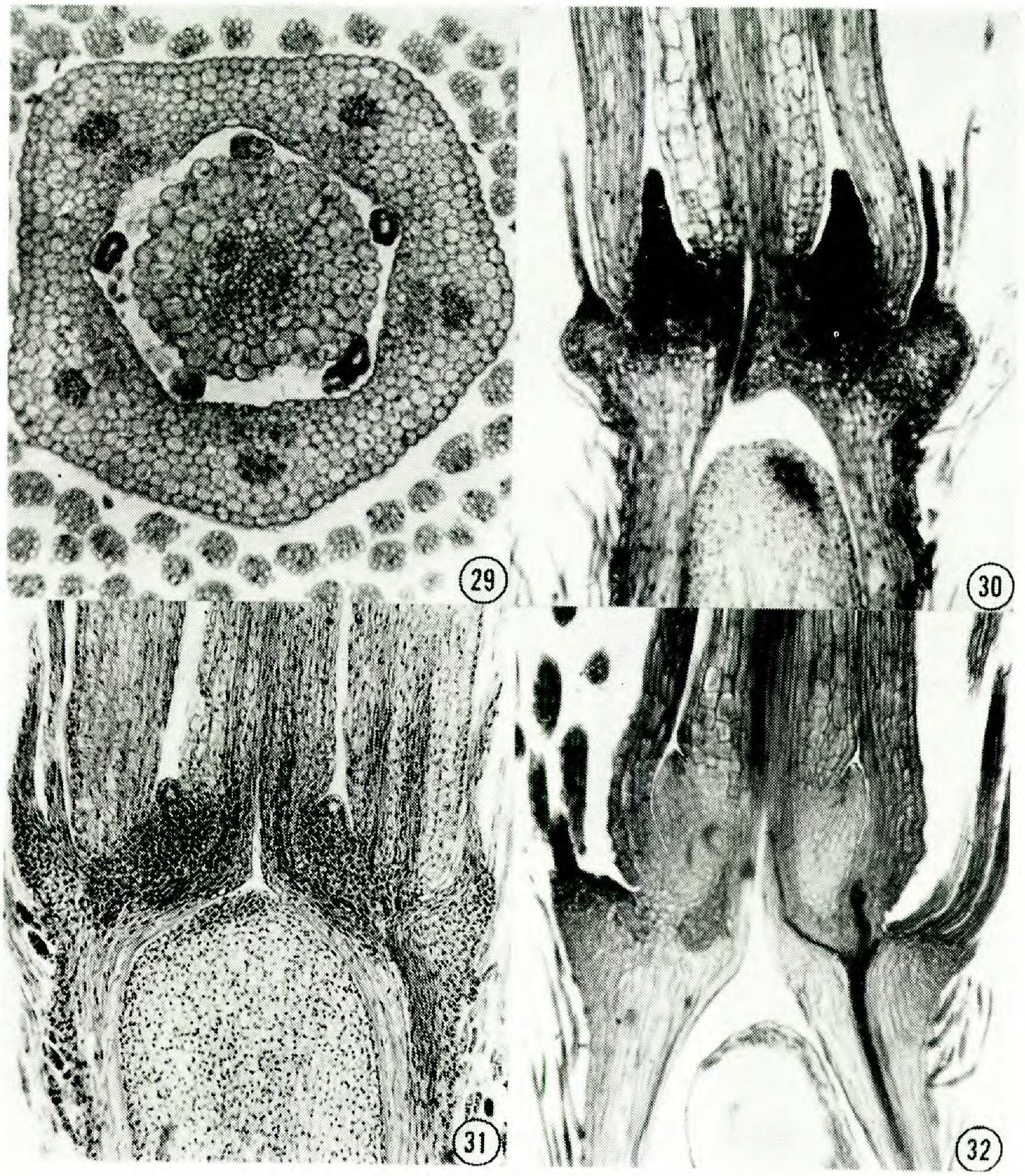


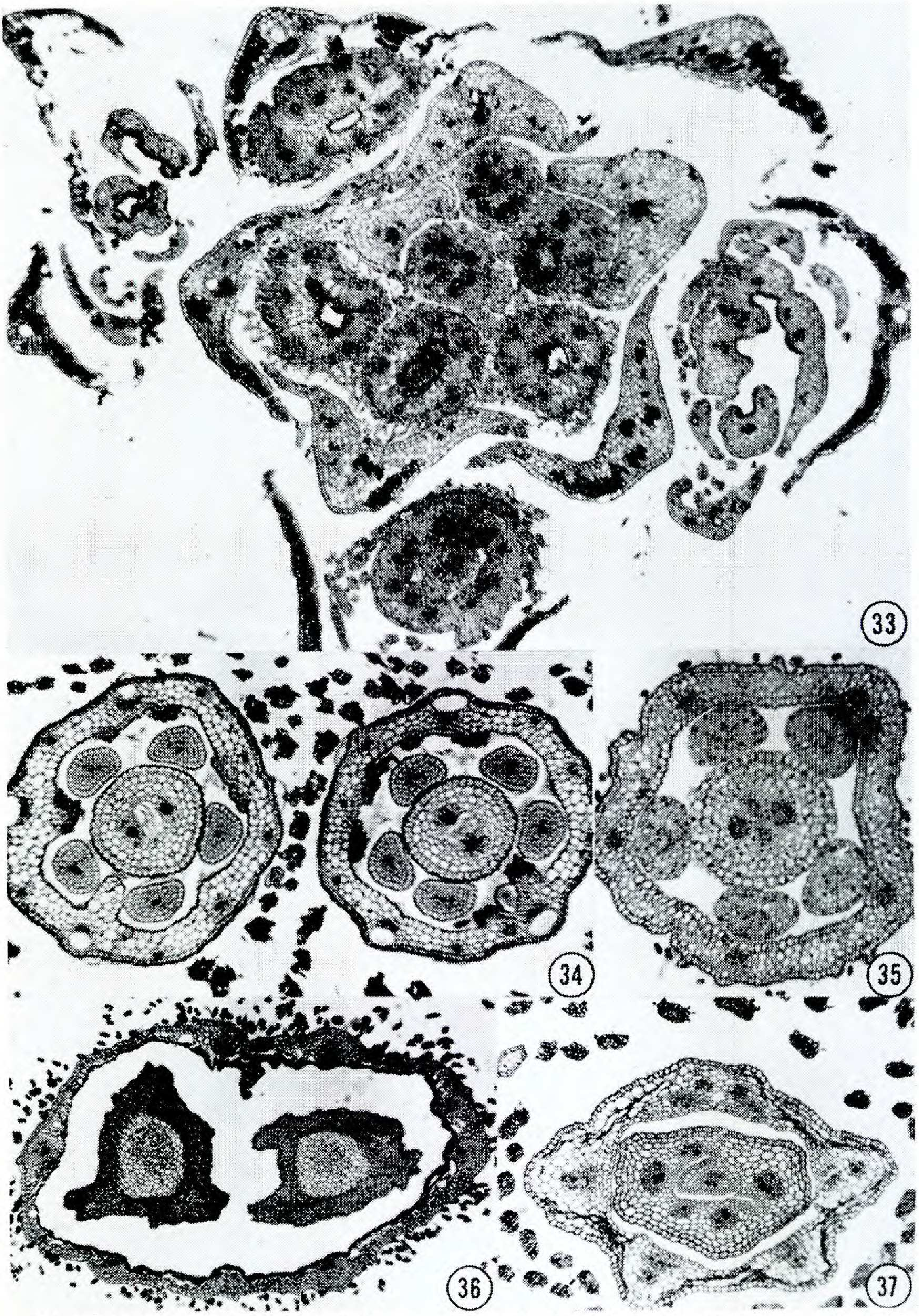
Fig. 24. Diagrammatic flower with stamens removed. Fine lines represent vasculature; broken lines, maximum secretory canal distribution. Roman numerals indicate zones to determine secretory canal abundance; see headings in Table 1. Letters A, B, and C are levels of corolla used to determine thickness (cell number) for Table 1.



Figs. 25—28. Transections of nearly mature achenes (cypselas). Fig. 25. *C. parryi* ssp. *parryi* (*A 1973*), note prominent sclereids of ovule wall. Fig. 26. *C. nauseosus* ssp. *albicaulis* (*A 1773*). Fig. 27. *C. spathulatus* (*A 3008*), sclereids of ovule wall less prominent, packets of sclerenchyma in ovary wall. Fig. 28. *C. pulchellus* (*A 3056*), most of ovary wall heavily sclerosed. Figs. 25—28, X 96.



Figs. 29—32. Nectaries. Fig. 29. Transection at corolla base of *C. nauseosus* ssp. *consimilis* (*A 1921*) showing five peaks of nectary ring around base of style. Fig. 30. Longisection of *C. paniculatus* (*A 1931*). Fig. 31. *C. humilis* (*A 2950*), glandular trichomes intermixed with twin-hairs on achene. Fig. 32. *C. parryi* ssp. *vulcanicus* (*A 2035*), note vascular trace to base of pappus in addition to those going to corolla and style. Fig. 29, X 105. Figs. 30—31, X 140.



Figs. 33—37. Teratological forms. Fig. 33. Head of *C. linifolius* (*A 1860*) with four abnormal flowers positioned among the phyllaries outside the central cluster of six. Fig. 34. Corolla transections of *C. viscidiflorus* ssp. *viscidiflorus* (*A 2714*) with five additional bundles (midveins) in the tube; secretory canals and abnormal growths (staminodes?) are associated with the additional bundles. Fig. 35. Corolla tube of *C. nauseosus* ssp. *salicifolius* (*A 977*) with unfused lateral bundles in upper right-hand corner. Fig. 36. Bicarpellate ovary of *C. humilis* (*A 1606*) with two ovules and a gynoecial bundle in the ridge of the ovule wall. Fig. 37. Corolla tube of same flower (*A 1606*) showing base of trifid style with six bundles; the central one is the gynoecial bundle of the achene in Fig. 36. Fig. 33, X 40. Figs. 34—37, X 145.

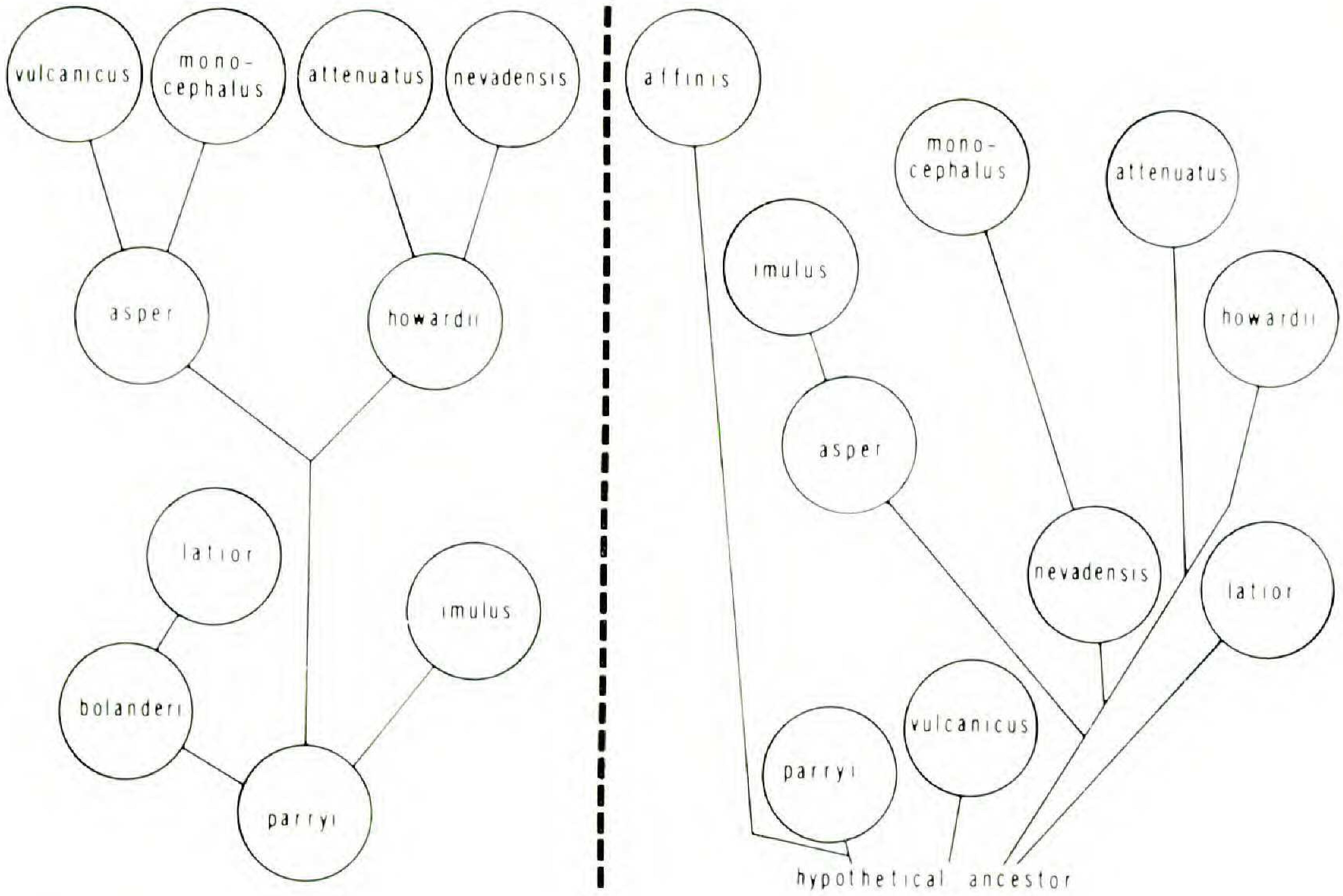


Fig. 38. Comparison of schemes on the infraspecific relationships in the *C. parryi* complex. Left—redrawn from Hall and Clements (1923) to illustrate their concept of phylogeny in the group. Right—my concept, based largely on data from floral anatomy; vertical spacing reflects degree of phylogenetic specialization.

TABLE 1. SELECTED FEATURES OF FLORAL ANATOMY IN CHRYSOTHAMNUS AND RELATED HAPLOPAPPUS

taxon and collections	*average flower number*	*ovarian bundle number*		*frequency of vascular patterns seen*					*secretory canal distribution*							*trichomes*									*corolla thickness*		
									achene		*corolla*				*style*	*achene*			*corolla tube*			*corolla lobe*					
		ave.	*rg.*	*a*	*b*	*c*	*d*	*e*	*I*	*II*	*III*	*IV*	*V*	*VI*	*VII*	*type*	*frequency*	*length, µ*	*type*	*frequency*	*length, µ*	*type*	*frequency*	*length, µ*	*A*	*B*	*C*
NAUSEOSI																											
C. parryi ssp. affinis A2465, A2771	5.0	6.0	5-7	0	0	1	0	1	0	+	0	++	++	−	++	n	++	560	g	++	209				7	5	2
(undescribed?) A1726, A1782	5.0	5.5	5-8	0	0	0	0	1	0	0	0	+	−	0	−	n	++	672	g n	+ −	224 291				7	5	2
ssp. asper A1683, A1919, A2024, A2043	5.4	8.5	7-10	2	1	1	0	0	−	+	+	+	++	−	++	n	++	414	g n	++ ++	177 427	n	−	800	8	5	2
ssp. attenuatus A988, A1523	5.3	7.2	5-8	0	0	4	1	0	−	+	−	++	+	0	+	n	++	504	g	++	181	n	+	530	8	5	2
(undescribed?) A1658, A1660, A1662	5.0	5.1	5-6	0	0	0	0	4	−	+	0	++	+	0	++	n	++	525	g n	++ −	118 358	n	−	480	7	5	2
ssp. howardii A1536, A2691, A2768	5.0	7.0	5-9	0	0	1	1	0	−	++	−	++	+	−	+	n	++	358	g	++	177	n	++	900	8	5	3
ssp. imulus A1923, Jones in 1900	10.0	9.1	8-10	1	0	0	0	0	0	+	0	+	0	0	+	n	++	410	n	+	287	n	++	750	7	5	2
ssp. latior A2945, A2949	5.0	9.7	8-11	2	0	0	0	0	+	++	−	++	++	−	++	n	++	571	g	+	188	n	−	92	8	5	2
ssp. monocephalus A2031, A2919	5.6	7.0	5-9	0	0	1	0	1	−	+	+	++	+	0	−	n	++	448	g n	+ −	145 314	n	−	490	7	5	2
ssp. nevadensis A1582, A2079, A2952	5.2	9.1	8-10	2	0	0	0	0	0	+	++	++	++	+	++	n	++	627	g n	++ +	286 538	n	++	1100	7	5	2
(undescribed?) A1561, A2966	3.0	5.3	5-6	0	0	0	0	1	0	+	+	++	++	0	−	n	++	548	g	++	150				7	5	2
ssp. parryi A912, A1818, A2526, A2681	12.2	9.7	8-11	2	4	4	2	0	++	++	+	++	++	++	++	n	++	488	g	++	225				7	5	2

Table 1. (continued—2)

					secretory canal distribution							trichomes											
					achene		corolla				style	achene			corolla tube			corolla lobe			corolla thickness		
taxon and collections	average flower number	ovarian bundle number ave.	rg.	frequency of vascular patterns seen a b c d e	I	II	III	IV	V	VI	VII	type	frequency	length, μ	type	frequency	length, μ	type	frequency	length, μ	A	B	C
(undescribed?) A1024	6.5	5.3	5-7	0 0 1 0 2	–	+	0	+	+	0	+	n	++	433	g	+	141				7	5	2
ssp. vulcanicus A1913, A2035	5.7	9.6	9-10	2 0 0 0 0	++	++	+	++	++	++	++	n	++	538	g	++	185	n	–	450	7	5	2
C. nauseosus ssp. albicaulis A1028, A1629, A1644, A1773, A2001, A2026, A2927	5.0	5.6	5-7	0 0 0 0 11	–	+	–	++	++	–	++	n	++	448	g n	++ –	167 251	n	–	375	7	5	2
ssp. bernardinus A1916, A2041	5.0	8.0	6-9	0 0 3 0 0	–	+	+	++	++	–	++	n	++	540	g	++	148				7	5	2
ssp. bigelovii A1850, A2432, A3051	5.0	5.7	5-6	0 0 0 0 1	–	+	–	++	++	–	++				g	+	167	n	+	520	6	5	2
ssp. ceruminosus A1934, A1939	5.0	5.2	5-6	0 0 1 1 2	–	+	0	+	++	0	++	n	++	229	g	++	145				7	5	2
ssp. consimilis A1570, A1623, A1027, A1832, A1921, A2470	5.0	5.0	5	0 0 0 0 12	–	+	0	++	++	–	++	n	++	448	g	++	145				6	4	2
ssp. graveolens A1799, A2422, A2513, A2720, A3012, A2999	5.0	6.0	5-8	0 0 1 0 3	–	+	–	++	++	0	++	n	++	352	g	++	169				7	5	2
ssp. hololeucus A1600, A1918, A1942	5.0	5.8	5-7	0 0 2 0 3	–	++	–	++	++	0	++	n	++	336	g	++	171				7	5	2
ssp. junceus A1696, A1748	5.0	5.1	5-6	0 0 0 0 1	–	+	0	++	++	0	++	n	++	571	g	++	112	n	+	240	6	4	2
ssp. latisquameus A3042, A3048	5.0	5.0	5	0 0 0 0 3	–	+	–	++	++	+	++	n	++	392	g	++	172				7	5	2

Table 1. (continued—3)

taxon and collections	*average flower number*	*ovarian bundle number*		*frequency of vascular patterns seen*					*secretory canal distribution*							*trichomes*									*corolla thickness*		
		ave.	*rg.*	*a*	*b*	*c*	*d*	*e*	*achene*		*corolla*			*style*		*achene*			*corolla tube*			*corolla lobe*			*A*	*B*	*C*
									I	*II*	*III*	*IV*	*V*	*VI*	*VII*	*type*	*frequency*	*length, µ*	*type*	*frequency*	*length, µ*	*type*	*frequency*	*length, µ*			
ssp. leiospermus A866, A1995, A2011	5.0	5.2	5-7	0	0	0	0	1	–	+	–	++	++	0	++				g	+	141				5	4	2
(undescribed?) A1739, A1752, A1753	5.0	5.4	5-7	0	0	0	0	1	–	+	0	++	++	0	++	n	–	224	g	+	250	n	–	595	6	4	2
ssp. mohavensis A1686, A1932	5.0	5.2	5-6	0	0	0	0	4	–	+	+	++	++	0	++	n	++	336	g	+	157				6	5	2
ssp. nanus Cronquist & Preece 6812, Yates 2	5.0	5.0	5	0	0	0	0	1	+	++	–	++	++	0	+	n	++	481	g	+	157				7	5	2
ssp. nauseosus A2578, A2707	5.0	5.0	5	0	0	0	0	1	–	++	+	++	++	0	++	n	++	435	g	++	142				5	4	2
ssp. psilocarpus A1531, A2070, A2886	5.0	5.8	5-6	0	0	2	0	1	–	+	0	++	++	0	+				g	++	121				6	5	2
ssp. salicifolius A977, A1009	5.0	6.9	5-8	0	0	2	0	1	0	++	0	++	++	0	++	n	++	448	g	++	160				7	5	2
ssp. turbinatus A884, A1729, A2530	5.0	5.3	5-7	0	0	1	0	3	0	+	–	++	++	0	++	n	++	442	g n	++ –	164 459	n	++	500	7	5	2
(undescribed?) A1771, A1778	5.0	10.4	10-12	0	1	0	0	0	+	++	–	++	++	0	++	n	++	347	g n	+ –	153 870	n	–	370	7	5	2
(undescribed?) A1756, A1849	5.5	11.2	10-12	0	1	0	0	0	+	++	0	++	++	0	++	n	++	426	g	+	204				7	4	2
ssp. viscosus Munz 12689 (RSA)	8.0	5.0	5	0	0	0	0	1	–	++	0	++	++	0	++	n	++	384	g	+	104				5	4	2

Table 1. (continued—4)

taxon and collections	average flower number	ovarian bundle number ave.	ovarian bundle number rg.	frequency of vascular patterns seen a	b	c	d	e	secretory canal distribution achene I	achene II	corolla III	corolla IV	corolla V	style VI	style VII	trichomes achene type	achene frequency	achene length, μ	corolla tube type	corolla tube frequency	corolla tube length, μ	corolla lobe type	corolla lobe frequency	corolla lobe length, μ	corolla thickness A	B	C
CHRYSOTHAMNUS																											
C. linifolius A1487, A1860, A2500, A2702, A2738	5.5	8.6	6-10	3	7	1	0	0	–	+	0	–	++	0	0	n	++	414							8	5	2
C. spathulatus A2052, A3008, A3022, A3209	5.0	6.2	5-9	0	0	1	4	2	0	–	0	0	++	0	0	n	–	138							8	6	3
C. albidus A853, A1586, A2963	5.0	7.1	5-10	0	0	0	2	0	0	0	0	0	0	0	0	n g	++ +	450 73							7	6	2
C. greenei A878, A1838, A2433	4.5	5.8	5-7	0	0	1	0	6	0	–	0	+	++	0	0	n	++	482							9	6	2
C. viscidiflorus ssp. elegans A1569, A1983, A2885	4.0	6.9	5-7,10	1	0	1	0	3	0	–	–	+	++	0	0	n	++	305	g	–	60				9	7	3
ssp. lanceolatus A1563, A2473, A2717, A2737, A2757, A2888	4.3	6.0	5-8	0	0	5	0	3	0	+	0	–	+	0	0	n	++	336	g	+	128				8	6	2
ssp. latifolius A1611, A1614	7.0	6.4	5-9	0	0	3	0	1	0	–	0	+	++	0	0	n	++	481							7	6	2
ssp. planifolius A1853, A2094	4.4	7.2	6-10	0	0	4	0	0	0	–	0	0	+	0	0	n	+	392							10	7	2
ssp. puberulus A1961, A2005 ,A2017	5.0	6.1	5-8	0	0	0	2	2	0	+	0	+	++	0	0	n	++	302							9	6	2
(undescribed?) A1935, A1936, A2055	5.0	5.0	5	0	0	0	0	4	0	–	0	+	++	0	0	n	++	402							9	6	3

Table 1. (continued—5)

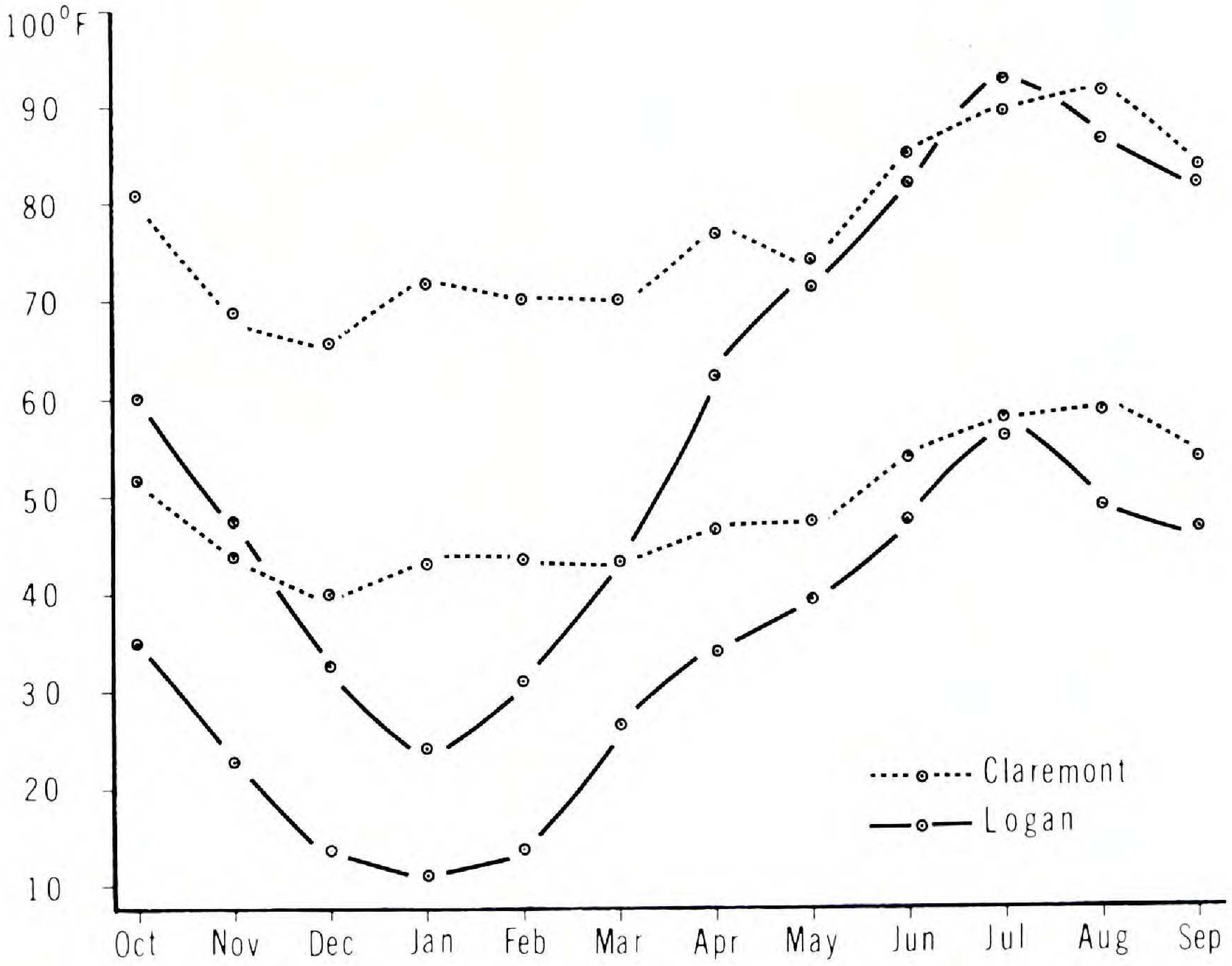
taxon and collections	average flower number	ovarian bundle number ave.	rg.	frequency of vascular patterns seen a	b	c	d	e	achene I	II	secretory canal distribution corolla III	IV	V	style VI	VII	trichomes achene type	frequency	length, µ	corolla tube type	frequency	length, µ	corolla lobe type	frequency	length, µ	corolla thickness A	B	C
ssp. pumilus A2692, A2701, A2730	4.3	6.2	5-8	0	0	2	1	1	0	+	0	+	++	0	0	n	++	336							8	6	3
ssp. stenophyllus A1746, A2087, A2737, Reveal 898, Reveal 1030	4.3	5.7	5-8	0	0	0	2	3	-	+	0	+	++	0	0	n	++	324							8	6	2
ssp. viscidiflorus A1701, A1922, A2004, A2669, A2714, A2756, A2944	5.0	6.5	5-8	0	0	6	1	3	-	+	-	+	++	0	0	n	++	325							8	6	3
C. humilis A1606, A2950, Sonne in 1835	3.0	6.1	5-8	0	0	2	0	4	0	-	0	+	++	0	0	g n	+ +	88 358	g n	++ -	105 190				9	7	3
PULCHELLI																											
C. vaseyi A936, A1002, A2743	5.4	7.2	5-10	0	0	3	1	3	0	+	-	++	++	0	0	g n	+ -	69 120							9	7	3
C. molestus A1840, A3148	5.5	8.0	6-9	0	0	2	2	0	++	++	-	+	++	0	0	g	+	95	g	+	85				10	7	3
C. depressus A935, A2147, A2515, A2676, A2909	5.0	8.1	7-10	1	0	1	1	0	-	+	0	++	+	0	0	g n	+ -	100 72							12	5	2
C. pulchellus A1764, A2590, A2995, A3054, A3055, A3213	5.0	6.0	5-7	0	0	0	3	3	-	+	0	+	+	0	0	n	-	213							8	6	2
PUNCTATI																											
C. teretifolius A1930, A1943, Reveal 64-13	5.0	5.8	5-6	0	0	1	1	2	0	-	-	++	-	0	++	n	++	396	g	++	105				7	5	2

Table 1. (continued—6)

taxon and collections	average flower number	ovarian bundle number		frequency of vascular patterns seen					secretory canal distribution							trichomes									corolla thickness		
									achene		corolla				style	achene			corolla tube			corolla lobe					
		ave.	rg.	a	b	c	d	e	I	II	III	IV	V	VI	VII	type	frequency	length, µ	type	frequency	length, µ	type	frequency	length, µ	A	B	C
C. paniculatus A1871, A1925, A1931	6.8	5.8	5-8	0	0	4	1	1	0	0	0	0	0	0	0	n	++	540	g	++	91				6	5	2
MACRONEMA (HAPLOPAPPUS)																											
H. bloomeri A2943	6.0	5.2	5-6	0	0	0	0	2	-	+	+	+	+	0	0	n	-	290	g	++	116				7	5	2
H. macronema A2540, A2922	20.0	6.1	5-7	0	0	1	0	1	++	++	+	++	++	0	+	n	++	392	g	++	221	g n	- -	164 255	7	5	2
H. ophitidus A2935	4.0	5.2	5-6	0	0	0	0	1	0	+	0	+	0	0	0	g n	— -	112 336	g	+	130	n	-	230	7	5	2
ERICAMERIA (HAPLOPAPPUS)																											
H. propinquus Moran 8495, Raven 16802 (RSA)	10.0	9.2	7-10	1	0	0	0	0	++	++	0	++	++	0	0	n	++	560	g	+	92	g	-	70	10	6	3
H. pyramidatus Smith 371 (POM)	11.0	2.0	2	0	0	0	0	0	0	0	0	+	0	0	0	n	++	205	g	+	145	g	++	107	7	5	2
H. sonoriensis Moran 8564	6.0	6.0	6	0	0	2	2	0	++	++	0	0	+	0	0	n	++	485	g	+	100				7	5	2
H. trianthus A3032	3.5	6.0	5-8	0	0	1	0	1	+	++	++	++	++	0	0	n	++	420	g	+	128				8	5	2

TABLE 2. ENVIRONMENTAL DATA FOR EXPERIMENTAL GARDENS

Temperatures, mean monthly maximums and minimums, for one year prior to harvest.



Garden	*Latitude*	*Elevation*	*Mean temperature*	*Precipitation*	*Soil pH*	*Soil description*
Logan	41° 46′	4850′	42.5°F	12.3″	7.7	strongly calcareous gravelly loam (Green Canyon series); substrate loose, gravelly sandy loam or loamy sand
Claremont	34° 04′	1350′	63.1°F	6.6″	7.4	very fine clay loam (San Jose series); substrate very tight hardpan and rocky clay

TABLE 3. ENVIRONMENTAL DATA FROM ORIGINAL COLLECTION SITES FOR PLANTS USED IN GARDEN STUDIES

Taxon	*Locality & Collection*	*Latitude*	*Elevation, feet*	*Ave. Annual Temperature, degrees, F.*	*Ave. Annual Precipitation, inches*
C. parryi					
ssp. attenuatus	Wasatch Co., Utah, *A988*	39° 56′	7450	39.0	15.9
ssp. parryi	Kane Co., Utah, *A1679*	37° 29′	7000	45.3	16.1
(undescribed ?)	Clark Co., Idaho, *A1024*	44° 28′	9500	E35.0	E19.4
C. nauseosus					
ssp. albicaulis	Lake Co., Oregon, *A1629*	42° 45′	4300	48.0	10.1
ssp. consimilis	Elko Co., Nev., *A1570*	41° 04′	5350	42.8	10.3
C. greenei	Millard Co., Utah, *A878*	38° 51′	5350	50.7	7.0
C. viscidiflorus					
ssp. viscidiflorus	Coconino Co., Ariz., *A1701*	36° 41′	6100	52.5	7.8
C. humilis	Humboldt Co., Nev., *A1606*	41° 53′	5700	E44.4	E6.8
C. vaseyi	Garfield Co., Utah, *A936*	37° 42′	8400	E40.2	13.7
C. depressus	Garfield Co., Utah, *A935*	37° 42′	8400	E40.2	13.7

E = estimated

TABLE 4. FLORAL ANATOMY OF CHRYSOTHAMNUS POPULATIONS GROWN IN THREE DIFFERENT ENVIRONMENTS

taxon and collections	*average flower number*	*ovarian bundle number*		*frequency of vascular patterns seen*					*secretory canal distribution*							*trichomes*									*corolla thickness*		
									achene		*corolla*				*style*	*achene*			*corolla tube*			*corolla lobe*					
		ave.	*rg.*	*a*	*b*	*c*	*d*	*e*	*I*	*II*	*III*	*IV*	*V*	*VI*	*VII*	*type*	*frequency*	*length, µ*	*type*	*frequency*	*length, µ*	*type*	*frequency*	*length, µ*	*A*	*B*	*C*
NAUSEOSI																											
C. parryi ssp. attenuatus																											
A988	7.0	6.6	5-8	0	0	2	1	0	–	+	0	++	+	0	+	n	++	560	g	++	175	n	+	670	7	6	2
Logan	5.0	6.6	6-7	0	0	3	1	0	–	+	0	++	–	0	+	n	++	580	g	++	190	n	–	460	8	6	2
Claremont	5.0	7.4	6-8	0	0	1	0	0	+	++	0	++	–	0	+	n	++	448	g	++	179	n	+	540	7	5	2
ssp. parryi																											
A1679	10.5	8.7	7-10	0	1	2	2	0	++	++	++	++	++	++	++	n	++	481	g	++	190				7	5	2
Logan	8.0	7.4	6-9	0	0	3	0	0	+	++	++	++	++	+	++	n	++	605	g	++	190				7	5	2
Claremont	7.7	7.8	6-10	2	2	9	2	0	+	++	++	++	++	+	++	n	++	515	g	++	198				7	5	2
(undescribed?)																											
A1024	6.5	5.3	5-6	0	0	1	0	2	0	+	0	+	+	0	+	n	++	433	g	+	135				7	5	2
Logan	8.0	5.2	5-7	0	0	0	0	1	+	+	0	+	+	0	+	n	++	465	g	+	148				7	5	2
Claremont	4.5	5.0	5	0	0	0	0	2	0	+	0	+	+	0	+	n	++	445	g	+	140				7	5	2
C. nauseosus ssp. albicaulis																											
A1629	5.0	5.8	5-7	0	0	1	0	1	+	++	+	++	++	0	++	n	++	400	g	++	195				7	5	2
Logan	5.0	5.6	5-7	0	0	0	1	1	+	++	+	++	++	+	++	n	++	336	g	++	143				7	5	2
Claremont	5.0	5.4	5-6	0	0	0	0	1	+	++	+	++	++	0	++	n	++	358	g	++	168				6	5	2

Table 4. (continued—2)

taxon and collections	average flower number	ovarian bundle number		frequency of vascular patterns seen					secretory canal distribution							trichomes									corolla thickness		
									achene		corolla				style	achene			corolla tube			corolla lobe					
		ave.	rg.	a	b	c	d	e	I	II	III	IV	V	VI	VII	type	frequency	length, µ	type	frequency	length, µ	type	frequency	length, µ	A	B	C
ssp. consimilis A1570	5.0	5.0	5	0	0	0	0	5	0	–	0	++	++	0	++	n	++	524	g	++	159				6	5	2
Logan	5.0	5.0	5	0	0	0	0	2	–	+	–	++	++	–	++	n	++	585	g	++	155				5	4	2
Claremont	5.0	5.0	5	0	0	0	0	3	0	–	0	++	++	0	+	n	++	470	g	++	153				6	4	2
CHRYSOTHAMNUS																											
C. greenei A878	4.5	5.0	5	0	0	0	0	1	0	+	0	++	++	0	0	n	++	481							9	6	2
Logan	4.0	5.2	5-6	0	0	0	0	1	0	+	0	++	++	0	0	n	++	594							9	7	2
Claremont	4.5	6.0	5-7	0	0	1	0	1	–	+	0	++	++	0	0	n	++	470							9	6	2
C. viscidiflorus ssp. viscidiflorus A1701	4.5	5.1	5-6	0	0	0	0	1	0	+	+	+	++	0	0	n	++	582							7	5	3
Logan	4.0	6.5	6-7	0	0	2	0	0	0	+	0	+	++	0	0	n	++	582							8	5	3
Claremont	5.0	6.2	5-8	0	0	1	0	0	0	+	+	++	++	0	0	n	++	570							8	5	3
C. humilis A1606	3.0	6.7	6-7	0	0	2	0	0	0	–	0	+	++	0	0	n g	+ +	215 99	g	++	111				9	6	3
Logan	3.0	7.3	7-8	0	0	1	0	0	0	–	0	+	++	0	0	n g	+ +	230 100	g	++	112				10	6	3
Claremont	3.5	5.2	5-6	0	0	0	0	2	0	–	0	+	++	0	0	n g	+ +	291 104	g	++	109				10	6	3

Table 4. (continued—3)

taxon and collections	average flower number	ovarian bundle number		frequency of vascular patterns seen					secretory canal distribution							trichomes									corolla thick-ness		
									achene		corolla				style	achene			corolla tube			corolla lobe					
		ave.	rg.	a	b	c	d	e	I	II	III	IV	V	VI	VII	type	frequency	length, μ	type	frequency	length, μ	type	frequency	length, μ	A	B	C
PULCHELLI																											
C. vaseyi A936	6.0	5.9	5-7	0	0	1	0	3	0	+	−	++	++	0	0	g n	+ −	65 119							9	7	4
Logan	5.0	7.4	7-8	0	0	1	0	0	0	−	+	++	++	0	0	g n	+ +	66 226							9	6	3
Claremont	5.0	6.7	6-8	0	0	1	0	0	0	+	+	++	++	0	0	g n	+ ++	71 347							9	6	3
C. depressus A935	5.0	8.2	8-10	1	0	0	1	0	0	+	0	+	+	0	0	g n	+ −	90 103							12	6	3
Logan	5.0	8.0	7-10	0	1	0	4	0	0	−	0	+	+	0	0	g n	+ −	87 115							11	6	3
Claremont	6.0	7.0	6-9	0	0	0	2	0	0	+	0	+	+	0	0	g n	+ −	67 112							12	6	3

TABLE 5. FLORAL FEATURES OF PUTATIVE HYBRIDS AND THEIR PARENTS

collection	*ave. flower number*	*ovarian trace number*		*secretory canal distribution*							*trichome length, μ*	*corolla thickness*		
		ave.	*rg.*	*I*	*II*	*III*	*IV*	*V*	*VI*	*VII*		*A*	*B*	*C*
C. parryi ssp. parryi *A2746*	10.7	10.0	10	++	++	++	++	++	++	++	g185	8	5	2
hybrid > C. parryi *A2747*	9.0	6.5	5-8	+	++	+	++	++	+	++	g199	7	5	2
hybrid — intermediate *A2748*	7.5	7.5	5-10	+	+	+	++	++	+	++	g167	7	5	2
hybrid > C. nauseosus *A2749*	6.0	7.3	6-9	+	+	0	++	++	++	++	g164	7	5	2
C. nauseosus ssp. nauseosus *A2745*	5.0	5.0	5	+	+	0	++	++	+	++	g141	6	5	2

TABLE 6. TYPE AND FREQUENCY OF FLORAL TERATOLOGIES

Taxon	total populations sampled	total heads sampled	total number heads with teratologies	*categories*				
				4-merous	*6-merous*	*unfused lateral veins*	*extra corolla veins*	*tristylous*
NAUSEOSI								
C. parryi	33	66	16	3	4	4	6	5
C. nauseosus	59	87	10	2	3	3	1	4
CHRYSOTHAMNUS								
C. linifolius	5	12	4	1	1	0	3	0
C. spathulatus	5	9	3	0	1	0	3	0
C. albidus	4	5	1	0	1	0	0	0
C. greenei	3	11	4	0	2	0	2	1
C. viscidiflorus	33	60	21	10	3	0	9	1
C. humilis	4	7	5	6	1	0	0	1
PULCHELLI								
C. vaseyi	3	7	4	0	1	0	3	0
C. molestus	2	2	0	0	0	0	0	0
C. depressus	4	7	3	1	2	0	1	0
C. pulchellus	9	10	2	0	1	0	1	0
PUNCTATI								
C. teretifolius	3	4	1	1	0	0	0	0
C. paniculatus	3	5	0	0	0	0	0	0
All taxa	170	292	74	24	20	7	29	12